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Variability and change in the west Antarctic Peninsula marine system: research priorities and opportunities

Sian F. Henley[1], Oscar M. Schofield[2], Katharine R. Hendry[3], Irene R. Schloss[4], Deborah K. Steinberg[5], Carlos Moffat[6], Lloyd S. Peck[7], Daniel P. Costa[8], Dorothee C. E. Bakker[9], Claire Hughes[10], Patrick D. Rozema[11], Hugh W. Ducklow[12], Doris Abele[13], Jacqueline Stefels[11], Maria A. Van Leeuwe[11], Corina P. D. Brussaard[14], Anita G. J. Buma[11], Josh Kohut[2], Ricardo Sahade[15], Ari S. Friedlaender[16], Sharon E. Stammerjohn[17], Hugh J. Venables[7], Michael P. Meredith[7]*

[1]School of GeoSciences, University of Edinburgh, James Hutton Road, Edinburgh, EH9 3FE, UK
[2]Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901, USA
[3]School of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK
[4]Instituto Antártico Argentino, Centro Austral de Investigaciones Científicas, Bernardo Houssay 200 (9410), Ushuaia, Tierra del Fuego, Argentina, and Universidad Nacional de Tierra del Fuego, Argentina
[5]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, USA
[6]School of Marine Science and Policy, University of Delaware, Newark, DE 19716, USA
[7]British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK
[8]Ecology and Evolutionary Biology Department, University of California Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA
[9]Centre for Ocean and Atmospheric Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK
[10]Environment Department, University of York, Heslington, York, YO10 5NG, UK
[11]University of Groningen, GELIFES, Nijenborgh 7, 9747 AG Groningen, The Netherlands
[12]Lamont-Doherty Earth Observatory, Columbia University, 61 Route 9W, Palisades, NY 10964, USA
[13]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
[14]Royal Netherlands Institute for Sea Research, 1790 AB Den Burg, Texel, The Netherlands
[15]Instituto de Diversidad y Ecología Animal, Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina
[16]Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University, Newport, OR 97365, USA
[17]Institute of Arctic and Alpine Research, University of Colorado, Campus Box 450, Boulder, CO 80309, USA

Corresponding author: s.f.henley@ed.ac.uk

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Abstract

The west Antarctic Peninsula (WAP) region has undergone significant changes in temperature and seasonal ice dynamics since the mid-twentieth century, with strong impacts on the regional ecosystem, ocean chemistry and hydrographic properties. Changes to these long-term trends of warming and sea ice decline have been observed in the 21st century, but their consequences for ocean physics, chemistry and the ecology of the high-productivity shelf ecosystem are yet to be fully established. The WAP shelf is important for regional krill stocks and higher trophic levels, whilst the degree of variability and change in the physical environment and documented biological and biogeochemical responses make this a model system for how climate and sea ice changes might restructure high-latitude ecosystems. Although this region is arguably the best-measured and best-understood shelf region around Antarctica, significant gaps remain in spatial and temporal data capable of resolving the atmosphere-ice-ocean-ecosystem feedbacks that control the dynamics and evolution of this complex polar system. Here we summarise the current state of knowledge regarding the key mechanisms and interactions regulating the physical, biogeochemical and biological processes at work, the ways in which the shelf environment is changing, and the ecosystem response to the changes underway. We outline the overarching cross-disciplinary priorities for future research, as well as the most important discipline-specific objectives. Underpinning these priorities and objectives is the need to better define the causes, magnitude and timescales of variability and change at all levels of the system. A combination of traditional and innovative approaches will be critical to addressing these priorities and developing a co-ordinated observing system for the WAP shelf, which is required to detect and elucidate change into the future.

Introduction

The west Antarctic Peninsula (WAP) continental shelf hosts a productive marine ecosystem, which is regionally important for krill stocks over the shelf and downstream in the Southern Ocean circulation system (e.g. Atkinson et al. 2004; Quetin et al. 1996), and for larger marine organisms as a breeding and/or feeding ground for migratory and year-round species (e.g. Costa and Crocker 1996; Ducklow et al. 2007; Friedlaender et al. 2006). From a climatic and biogeochemical perspective, the WAP is important because the southern flank of the Antarctic circumpolar current (ACC) flows particularly close to the shelf edge in this region (Orsi et al. 1995). As such, circumpolar deep water (CDW) from its mid-depths incurs directly on to the shelf in a less modified form than elsewhere around Antarctica, facilitating greater connectivity and exchange of physical and biogeochemical properties between these intermediate water masses and the atmosphere and surface ocean (Hofmann et al. 1996; Klinck 1998). Significant variability in the physical environment, modulated by strong coupling to climate processes over interannual and decadal timescales, is having a strong impact on regional biogeochemistry and all levels of the shelf ecosystem, making the WAP an important model region in which to understand the impacts of climate on polar marine systems.

Temperature records for the WAP have shown the largest average atmospheric warming in the southern hemisphere during the twentieth century, with particularly pronounced warming during winter (King et al. 2003; Vaughan et al. 2003). This has been accompanied by a significant decadal warming of surface and deeper waters and changes in salinity over large parts of the WAP shelf (Meredith and King 2005). Significant warming and salinification of the deeper waters over the southern and central WAP shelf resulted from shoaling of the thermocline along the slope and increased transport of warm upper circumpolar deep water (UCDW) onto the shelf, as well as increased heat content of the UCDW layers themselves (Martinson et al. 2008; Schmidtko et al.

2014). Significant surface freshening has been observed closer to coastal glacial meltwater sources, whilst upper layer salinification has occurred further offshore (Bers et al. 2013; Meredith and King 2005; Schloss et al. 2012).

Atmospheric and oceanic warming trends have been accompanied by strong changes in ice dynamics along the WAP, with the regional extent and duration of sea ice cover declining significantly since the late 1970s (Stammerjohn et al. 2012). Climate change appears more advanced in the northern region of the WAP as the warmer maritime climate moves southwards displacing the colder drier continental climate that dominated previously (Ducklow et al. 2007; Montes-Hugo et al. 2009). Substantial and widespread glacial retreat along the WAP has been attributed primarily to increasing ocean temperatures (Cook et al. 2016; Padman et al. 2012), with an important role for atmospheric forcing in the northern WAP (Falk and Sala 2015).

Whilst the regional warming and sea ice declines have been particularly rapid since the mid-twentieth century, these trends have slowed and plateaued since the late 1990s (Figure 1), with an absence of statistically significant atmospheric warming and sea ice losses between 1999 and 2014 (Turner et al. 2016). Statistically significant increases in sea ice extent have been observed in the northern WAP since the late 1990s (Turner et al. 2016), and an increase in both the extent and duration of sea ice cover, and its interannual variability, have been observed in the coastal WAP since the late 2000s (Figure 1; Schofield et al. 2017). These recent short-term reversals and the plateauing of longer-term trends reflect significant natural internal variability in the regional climate superimposed on longer-term trends, which leads to substantial short-term variation in sea ice dynamics (Hobbs et al. 2016; Stammerjohn and Maksym 2017; Turner et al. 2016). Whilst the plateauing of temperature and sea ice trends has weakened the magnitude of the longer-term trends, the overall warming and sea ice losses are still statistically significant (Figure 1).

Large-scale atmospheric circulation patterns and in particular the Amundsen Sea Low (ASL) exert a strong control on the observed climatic variability and change at the WAP (Raphael et al. 2016). The ASL is a persistent low pressure region between the Ross Sea and the Bellingshausen Sea/WAP sector, which is strongly influenced by the Southern Annular Mode (SAM) and also by the El Niño Southern Oscillation (ENSO) (Lachlan-Cope et al. 2001; Raphael et al. 2016; Turner et al. 2013). Changes in the ASL affect the strength and direction of winds over the WAP, which act as a key control on the amount and meridional extent of sea ice (Turner et al. 2013). A deepening ASL over the second half of the twentieth century, associated with positive SAM and more persistent La Niña phases, generated stronger north-to-northwesterly winds that advect warm moisture-laden air from the north and drive sea ice to the south, creating warm, low-ice conditions over the WAP and increasing precipitation (Turner et al. 1997). The recent plateauing of temperature and sea ice trends is associated with periods of more neutral to negative SAM phases, or positive SAM offset by El Niño, that promote cyclonic to anticyclonic conditions east to west of the peninsula, respectively, leading to more frequent cold east-to-southeasterly winds over the WAP and increased ice extent (Meredith et al. 2016; Stammerjohn et al. 2008; Turner et al. 2016). The combination of short-term internal variability and longer-term changes in atmospheric and ocean circulation patterns responding to global climate change complicates future projections of Antarctic sea ice, both at WAP and circumpolar scales (Turner and Comiso 2017). Understanding the extent to which the long-term trend of atmospheric warming and declining sea ice will continue in future, and the timescales over which different forcings are relevant, are leading-order challenges for the WAP scientific community.

The pronounced variability and change observed in atmospheric forcing, sea ice dynamics, glacial retreat, freshwater distribution and ocean physics along the WAP have a strong impact on primary production, community composition, ecosystem functioning, ocean chemistry and ocean-atmosphere exchanges of heat and dissolved gases (e.g. Ducklow et al. 2013; Meredith et al. 2017;

Venables and Meredith 2014). Improving our understanding of this dynamic system is of high scientific priority as a result of significant variability and change in the physical environment, important biological and biogeochemical consequences, and documented sensitivity to – and feedbacks on – climate change. The documented responses of ocean chemistry and biology to changes in climate and ocean physics make the WAP shelf region a unique model system for assessing how changes in climate might restructure ecosystems here and in other polar regions where sea ice changes are underway or expected in future. This importance is one of the key reasons why the WAP shelf region is the focus of a large international research effort, with a number of long-term records and spatially-extensive studies that are unparalleled around Antarctica. There are over thirty research stations along the WAP, either permanent or summer only, and a number of research ships that frequent the region, predominantly during summer.

Figure 2 shows the major sustained research efforts along the WAP, delineation of the northern, central and southern sub-regions referred to in this paper, and the major circulation and bathymetric features of the shelf system. The US Palmer Antarctica Long-Term Ecological Research (LTER) project has been in operation since 1990, and consists of spring/summer time-series sampling adjacent to Palmer Station, Anvers Island, and an annual summer cruise occupying a grid of stations over the WAP shelf between Anvers and Charcot Islands. The US National Oceanic and Atmospheric Administration Antarctic Marine Living Resources (AMLR) program has been active around the South Shetland Islands in the northern WAP since 1986, conducting annual research surveys and land-based field measurements with a focus on ecosystem-based management of fisheries, primarily krill. Since 1997, the Rothera Time Series (RaTS) of the British Antarctic Survey, located in Ryder Bay, northern Marguerite Bay adjacent to Rothera Research Station on Adelaide Island, has made year-round quasi-weekly measurements of physical and biogeochemical oceanographic parameters, benthic ecology and sea ice cover, with a large number of linked and complementary studies conducted by UK and international partners. The establishment of additional laboratories at Rothera by the Netherlands Organisation for Scientific Research (NWO) in 2012 increased the Dutch research effort in the WAP region substantially. The Argentinian Antarctic Program consists of time-series and process studies at a number of research stations along the WAP, as well as ship-based campaigns across the shelf. Year-round time-series monitoring of hydrographic and biological variables in Potter Cove, King George Island/ Isla 25 de Mayo, South Shetland Islands, has been conducted fortnightly-monthly since 1991, based at Carlini Station, which has been in operation since 1982. A joint Argentinian-German research program at Dallmann Laboratory on Carlini Station focusing on Potter Cove started in 1994, and forms an important part of the German research efforts in the WAP region, coordinated by the Alfred Wegener Institute (AWI). The Chilean Antarctic Institute (INACH) conducts scientific research programs at four bases along the WAP, supported by the Armed Forces. Chilean base Yelcho on Doumer Island was reopened in 2015 and there are plans to reopen Base Carvajal on Adelaide Island to complete a latitudinal transect from King George Island to Adelaide Island, as well as developing a long-term monitoring program. The Peruvian National Antarctic Program comprises summertime studies at Machu Picchu Research Station on King George Island, which was established in 1989, and oceanographic cruises. Spanish research programs centre on Juan Carlos I and Gabriel de Castilla Stations in the South Shetland Islands, which were opened in the late 1980s, as well as ship-based research. Brazilian research efforts have been underway in the northern WAP since the 1980s, with dedicated ship-based monitoring programs conducted through a number of initiatives coordinated by the Brazilian Antarctic Program since 2000. Chinese monitoring programs at Great Wall Station on King George Island have been in operation as part of the Chinese National Antarctic Program since the base was established in 1985. The Korea Polar Research Institute (KOPRI) runs a year-round marine ecosystem monitoring program in operation since 1996 at King Sejong Station on King George Island, which was inaugurated in 1988. The Henryk Arctowski Polish Antarctic Station, which opened in 1977 and is managed by the Institute of

Biochemistry and Biophysics of the Polish Academy of Sciences, has also served as a base for a number of marine studies around King George Island.

The Southern Ocean Observing System (SOOS) is an international organisation supported by the Scientific Committees on Antarctic Research (SCAR) and Oceanic Research (SCOR), which aims to co-ordinate Southern Ocean research, disseminate key findings and identify future directions and priorities (Meredith et al. 2013). The WAP working group of SOOS aims to bring together the different national programs, initiatives and projects working in the Peninsula region to maximise the science output across the spectrum of WAP marine research activities, to improve coordination and collaboration amongst ongoing research efforts, and to instigate and promote future developments and progress by identifying key gaps and opportunities to be addressed by future research. In this paper, we summarise the current state of knowledge under two high-priority overarching questions in WAP marine science:

1) What are the key mechanisms and interactions regulating ecosystem functioning and ocean-atmosphere coupling along the WAP shelf?

2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-climate feedbacks on the changes underway?

We take a whole ecosystem approach and consider the full range of dynamics and interactions from sea ice and water properties and circulation through phytoplankton dynamics and ocean biogeochemistry to pelagic, benthic and microbial food webs. We then discuss the most significant challenges and key overarching priorities for the international scientific community within the framework of these two questions, and present a model for an observing system for the WAP based on sustained observations of key variables and detailed process studies that will allow us to address these priorities. Figure 3 summarises the current state of knowledge of the key components of the WAP marine system and the most important mechanisms and interactions in the context of the two overarching questions outlined above, as well as the major priorities and approaches for future marine research at the WAP.

1) What are the key mechanisms and interactions regulating ecosystem functioning and ocean-atmosphere coupling along the WAP shelf?

1.1. Physical oceanography

The hydrography and circulation of the WAP shelf are influenced by intrusions of oceanic water from the ACC, inflow around the tip of the Peninsula from the Weddell Sea, and coupling with the atmosphere, cryosphere and land (Klinck et al. 2004; Martinson et al. 2008). Modulated by shelf dynamics, these processes lead to significant spatial and temporal property gradients in this region. Large seasonal variability occurs in surface waters, driven by strong heat loss and ice growth and advection in autumn and winter that leads to the formation of a deep winter mixed layer, and ice melting and partial restratification during spring and summer (Klinck et al. 2004; Meredith et al. 2008). Precipitation, glacial melt and sea ice melt modulate the freshwater content and stratification of the surface layer, with significant variability driven by ENSO and SAM over interannual timescales (Meredith et al. 2010; Meredith et al. 2017). A main feature of the surface circulation is the Antarctic Peninsula Coastal Current (APCC), a seasonal buoyancy- and wind-forced surface current, which flows southwestwards along the coast south of Anvers Island and west of Adelaide and Alexander

Islands during summer and autumn with a cyclonic circulation inferred within Marguerite Bay (Beardsley et al. 2004; Moffat et al. 2008; Savidge and Amft 2009).

The deep circulation and properties, particularly in the southern and central WAP, are strongly influenced by the proximity of the ACC to the shelf break, and by shelf topography and vertical mixing with the upper layers (Klinck 1998; Klinck et al. 2004; Martinson et al. 2008; Orsi et al. 1995). The CDW that resides in the mid-depths of the ACC is the main source of heat, salt, macronutrients and carbon for the subsurface shelf waters. Observational studies have revealed that CDW intrusions move across the shelf as small (~5 km wide) subsurface eddies, and are transported preferentially in deep, glacially-scoured submarine troughs that cross-cut the shelf (Couto et al. 2017; Martinson and McKee 2012; Moffat et al. 2009). Numerical models of the region have recently become eddy-resolving and revealed that shoreward transport can be expected via several of these troughs (Graham et al. 2016). The available observational evidence points to only weak seasonal variability in deep water properties, with synoptic-scale intrusion of eddies and other intraseasonal variability dominating instead (Martinson and McKee 2012; Moffat et al. 2009). The intruding waters cool and freshen on the shelf due to mixing with overlying waters and heat loss to the surface layer and atmosphere. Although the drivers of modification and vertical ventilation of CDW remain poorly understood, recent observations suggest that flow-topography interactions along the deep troughs constitute a key mechanism for vertical mixing (Venables et al. 2017). Mean upward heat fluxes from modified CDW to the surface layer are small (on average ~1 W/m^2), with stronger fluxes observed in early spring shortly after the first seasonal retreat of sea ice, but before the upper layer is strongly restratified (Brearley et al. 2017). Both of these processes highlight the importance of small-scale spatial (<1 km) and temporal (days to weeks) variability in controlling mixing rates and water modification at the WAP.

Bransfield Strait in the northern WAP differs markedly from the shelf to the south, with deep properties being modulated by colder, fresher waters originating in the Weddell Sea (Gordon and Nowlin 1978; Hofmann et al. 1996; van Caspel et al. 2018). The circulation in Bransfield Strait is generally cyclonic, with southward flow along the WAP coast and then turning towards the South Shetland Islands (Sangra et al. 2011; Zhou et al. 2002). A significant temperature gradient exists across Bransfield Strait, with warmer waters around the South Shetland Islands than along the mainland. The strong contrast in deep properties between Bransfield Strait and the shelf to the south suggests that deep water exchange between these two basins is limited (Hofmann et al. 1996), although its magnitude, temporal evolution, and dynamics are not fully described and understood.

1.2. Phytoplankton community dynamics

1.2.1. Pelagic primary production

The WAP shelf is a productive marine ecosystem, where primary production varies significantly in time and space, due to its regulation by upper ocean physics, light availability and the supply of macro- and micronutrients. As well as the role of phytoplankton in taking up nutrients and carbon dioxide, thus mediating air-sea gas exchange and larger-scale biogeochemical cycling, these primary producers constitute a critical food source for the entire WAP shelf ecosystem. High-biomass phytoplankton blooms occur during spring and summer (Hart 1942; Nelson and Smith 1991; Prézelin et al. 2000; Smith et al. 2008), when solar illumination increases and sea ice has retreated, leaving an exposed ocean surface (Moline and Prézelin 1996; Smith and Stammerjohn 2001). There is a strong productivity gradient with high productivity (~1000 mg C m^{-2} d^{-1}) inshore compared with offshore waters (~100 mg C m^{-2} d^{-1}) (Vernet et al. 2008). Seasonal satellite studies and *in situ* measurements show that net community production peaks first offshore and follows the inshore retreat of the sea ice (Arrigo et al. 2017; Li et al. 2016). The magnitude of primary productivity on an annual basis is

linked to climate modes such as ENSO and SAM, and their effect on the ASL, which influence the amount of sea ice present in the winter (Stammerjohn et al. 2008a), and this in turn affects primary productivity in the following spring and summer seasons (Saba et al. 2014). The duration of winter sea ice and the extent of winter wind-driven mixing, combined with the timing of ice retreat and mixing during spring, has been shown to control upper ocean stability during spring and summer, thus preconditioning the water column for phytoplankton growth (Venables et al. 2013; Saba et al. 2014; Schofield et al. 2017; Rozema et al. 2017a). In high-ice years, less wind-induced mixing over winter and a subsequent strong seasonal melt results in a more stable water column that retains phytoplankton in a shallower surface layer, where light conditions are favourable for growth (Moline 1998; Vernet et al. 2008; Carvalho et al. 2016). In low-ice years, enhanced wind-driven mixing and subsequently deeper mixed layers, combined with a smaller input of meltwater to restabilise the upper ocean, result in phytoplankton cells being mixed over a greater depth interval, experiencing lower light levels overall, such that primary productivity is reduced (Figure 4). Superimposed on the seasonal bloom dynamics are shorter-lived phytoplankton blooms (days-week) facilitated by periods of low wind that lead to increased water column stability (Moline 1998; Vernet et al. 2008; Carvalho et al. 2016). High primary productivity supports a productive food web that is tightly coupled to the seasonal phytoplankton dynamics, suggesting strong bottom-up control of the ecosystem (Saba et al. 2014).

While WAP phytoplankton communities are often dominated by diatoms, other taxa are increasingly recognised as important components of the food web. The importance of nanoplankton (<20 µm) and picoplankton (<2 µm) has been documented, with cryptophytes being the dominant nano-flagellate over much of the region (e.g. Krebs 1983; Buma et al. 1991; Kopczynska 1992; Garibotti et al. 2003; Varela et al. 2002; Rodriguez et al. 2002). Other major phytoplankton taxa include mixed flagellates and haptophytes, with haptophytes (e.g. the prymnesiophyte *Phaeocystis antarctica*) being more prominent than cryptophytes in Marguerite Bay (Garibotti et al. 2003; Kozlowski et al. 2011; Rozema et al. 2017a; Stefels et al. 2018). *P. antarctica* dominated the phytoplankton community during spring 2014 in the central WAP prior to the peak of the diatom bloom (Arrigo et al. 2017). During high-chlorophyll years, the late-spring/summer phytoplankton community is dominated by larger cells, primarily diatoms, with only a minor contribution from smaller size classes, primarily haptophytes and cryptophytes (Moline et al. 2004; Rozema et al. 2017a; Schofield et al. 2017; Schloss et al. 2014). In low-ice low-chlorophyll years, the haptophyte and cryptophyte contributions increase, whilst the diatom contribution is reduced. Cryptophyte abundance increases when a shallow meltwater lens, probably of glacial origin, overlies a well-mixed upper water column (Mura et al. 1995; Moline et al. 2004). Cryptophytes take up less CO_2 per unit chlorophyll than diatoms, such that a greater cryptophyte contribution may lead to reduced carbon uptake compared to diatom-dominated assemblages (Schofield et al. 2017).

Whilst the factors influencing phytoplankton community composition remain poorly understood, it is possible to segregate the presence and abundance of cryptophytes and diatoms at Palmer Station in temperature-salinity phase space (Figure 5a) (Schofield et al. 2017). Diatoms were observed over the full range of observed salinities and temperatures, with their abundance being significantly lower in colder and lower-salinity waters. Conversely, cryptophytes were most abundant in lower-salinity colder waters (-1 to 1° C), and absent at higher temperatures and salinities. The segregation of major phytoplankton taxa based on water mass properties at Palmer Station is not robust at the wider shelf scale (Figure 5b), since ship-based surveys indicate a range of cryptophyte species across the WAP that can occupy a range of hydrographic niches.

1.2.2. Coupling between sea ice and pelagic ecosystems

As well as regulating phytoplankton productivity through its control on upper ocean physics, sea ice can also play an important role in seeding the pelagic community. Primary production rates in Antarctic sea ice are highly variable, ranging from 0.5 to 1250 mg C m^{-2} d^{-1} (Arrigo 2017), and reaching maxima in spring and summer, when ice algae can contribute up to 50-60 % of total primary production in a given area (e.g. McMinn et al. 2010). The direct coupling between sea ice and pelagic ecosystems varies seasonally, according to ice extent and its productivity compared to underlying waters. When ice melts in spring, release of algal cells into the water column can initiate under-ice algal blooms (Lizotte 2001), although differences in species composition between sea ice and water column communities have been documented (e.g. Riaux-Gobin et al. 2011). The timing and pulse size of release act as strong controls on the fate of sympagic (ice-associated) algae (Selz et al. 2018), with a rapid early release contributing substantially to pelagic production, and a later release being more likely to be consumed by pelagic zooplankton or benthic communities (e.g. Riebesell et al. 1991).

Antarctic sympagic algae are an important food source for zooplankton, such as juvenile krill (Kohlbach et al. 2017) and various life stages of copepods (Bluhm et al. 2017). This is especially the case during winter, when chlorophyll concentrations in bottom sea-ice layers close to the ice-water interface can be 10 to 100-fold higher than in the underlying seawater. At the WAP, bottom-ice chlorophyll increased from ~5 µg L^{-1} to ~500 µg L^{-1} from September to December 2014 in land-fast ice adjacent to Rothera Station (Meiners et al. *in press*).

Export of ice-associated organic carbon, that is not remineralised in the sea ice or surface waters, to benthic ecosystems occurs at rates determined by its composition (Riebesell et al. 1991) and the dynamics of ice retreat (e.g. Norkko et al. 2007; Wing et al. 2012). Whilst organic carbon fluxes during ice-covered seasons are small compared to summertime fluxes along the WAP, sea ice algae are most relevant for local and episodic inputs preceding pelagic blooms, and in providing source material that is remineralised in winter to support detritus feeders (Mincks et al. 2005). Biogenic particle fluxes beneath land-fast sea ice were ~0.2 g m^{-2} d^{-1} during winter at King George Island/ Isla 25 de Mayo (Khim et al. 2007), and would be expected to increase dramatically during ice melt in spring. In the Ross Sea, tracer analysis shows that sea ice organic carbon fluxes can contribute >50 % of the total diet of Antarctic benthic organisms (Wing et al. 2012).

1.3. Nutrient biogeochemistry

The supply and cycling of inorganic and organic macro- and micronutrients along the WAP is regulated by physical and biological processes, and influences the spatial and temporal variation in production and ecosystem structure. Inorganic macronutrients are supplied to WAP shelf ecosystems primarily by CDW intruding onto the shelf from the ACC (Klinck et al. 2004; Prezelin et al. 2000). Cross-shelf transport of CDW in deep glacially-scoured canyons increases the supply of nutrients to biota in overlying waters, as well as increasing heat flux and reducing sea ice coverage, such that phytoplankton biomass is higher and more diatom-dominated over the canyons compared with adjacent shelf areas (Kavanaugh et al. 2015). The supply of inorganic nitrogen and silicic acid from sea ice is small compared to CDW, and dominated by regenerated nutrients (Fripiat et al. 2015; Henley et al. 2017). Phosphate accumulates in sea ice (Fripiat et al. 2017), but its effect on water column phosphate and micronutrient inventories remains unclear (Hendry et al. 2010). A glacial source of silicic acid in basal meltwater has been demonstrated around Greenland (Hawkings et al. 2017), and warrants investigation along the WAP.

Vertical nutrient fluxes from the modified CDW source into the surface ocean vary substantially in space and time. Vertical nitrate fluxes during summer in Marguerite Bay and along Marguerite Trough were estimated as 0.18 ± 0.17 mmol NO_3 m^{-2} d^{-1} with a maximum of 0.56 mmol NO_3 m^{-2} d^{-1}

(Henley et al. 2018). The mean summertime vertical nitrate flux for the Palmer LTER grid for 1998-2007 was estimated as 1.36 ± 1.79 mmol NO_3 m^{-2} d^{-1} (Pedulli et al. 2014), although the latter study used a uniform value for the vertical eddy diffusivity (K_z) that is likely to overestimate fluxes. Seasonal variability is poorly constrained, although vertical nutrient fluxes are expected to be greatest following the initial retreat of sea ice, in agreement with heat fluxes (Brearley et al. 2017). Whilst macronutrients are normally replete in WAP surface waters, intense biological drawdown by phytoplankton can lead to transient nutrient limitation in coastal areas during some summers (Henley et al. 2017). Interannual variability in CDW-derived nutrient supply is attributed to the degree of wintertime mixing at Palmer Station (Kim et al. 2016), but this cannot fully account for the observed variability at Rothera (Henley et al. 2017).

The degree of summertime surface ocean macronutrient depletion shows an onshore-offshore gradient driven by higher primary production in inshore regions (Pedulli et al. 2014). Seasonal nutrient drawdown during summer follows interannual variability in chlorophyll, sea ice and upper ocean conditions, such that high-ice, high-chlorophyll years lead to greater nutrient drawdown than lower-chlorophyll years (Figure 4) (Henley et al. 2017; Kim et al. 2016), with the potential to influence WAP shelf nutrient budgets and exports. In the coastal regions, the summer N/P uptake ratio varies between ~13, indicative of diatom-dominated phytoplankton communities under bloom conditions, and ~21, indicative of communities dominated by non-diatom phytoplankton and/or lower productivity conditions (Clarke et al. 2008; Henley et al. 2017; Kim et al. 2016). The summer Si/N uptake ratio is usually ≥1 in the Rothera and Palmer time series, indicating diatom-dominated production in these coastal regions (Henley et al. 2017; Kim et al. 2016). Nutrient uptake varies significantly within a season, due to changes in water column structure, sea ice and phytoplankton communities (Hendry et al. 2009). For example, time-series analyses of the stable silicon isotope composition ($\delta^{30}Si$) of silicic acid from northern Marguerite Bay show strong silicic acid drawdown by diatoms, interspersed with wind-driven mixing events that replenish the silicic acid reservoir from underlying waters (Cassarino et al. 2017).

Nitrate, phosphate and inorganic carbon are progressively enriched in subsurface waters as CDW moves across the shelf, and the stable nitrogen ($\delta^{15}N$) and oxygen ($\delta^{18}O$) isotope composition of nitrate (Figure 6) and nutrient stoichiometry show that this is driven by local remineralisation of organic matter and nutrient recycling in the upper water column (≤200 m) (Henley et al. 2017, 2018). Nitrification (regeneration of nitrate via ammonium oxidation) occurs in the deeper darker part of the euphotic layer, making the regenerated nitrate contribution to surface ocean primary production sensitive to whether the base of the euphotic layer resides within the mixed layer. Nitrate and phosphate regenerated in subsurface shelf waters, as opposed to that supplied from the CDW source, can account for up to one third of the surface ocean nutrient pools during summer, with implications for new production, net CO_2 uptake and organic matter export. Silicic acid is also enriched across the shelf, with maximum enrichment at depth (Henley et al. 2018). This indicates biogenic silica dissolution occurring deeper in the water column than organic matter remineralisation, and potentially in sediment porewaters, driving a return flux of silicic acid to the water column. New porewater silicon isotope data provide evidence for down-core changes in silicic acid being driven by dissolution of diatom frustules and potentially reverse weathering reactions (Cassarino et al. *in prep*).

Our understanding of organic nutrient budgets and cycling is more limited. Dissolved organic carbon (DOC) and nitrogen (DON) concentrations are low in the Southern Ocean compared to other ocean regions, with a labile to semi-labile pool in the upper ocean and a large refractory pool in CDW (Hansell et al. 2009; Kirchman et al. 2009; Ogawa et al. 1999). Low DOC concentrations and low bacterial production rates and biomass along the WAP suggest that bacterial production may be

limited by the availability of dissolved organic matter (DOM) (Ducklow et al. 2012a; Kim et al. 2016), but this is yet to be fully understood.

The essential micronutrient iron is supplied to the WAP surface ocean primarily from glacial meltwater and shallow sedimentary sources (Annett et al. 2015; Annett et al. 2017; Bown et al. 2018; Monien et al. 2017; Sherrell et al. 2018). Iron concentrations are replete in inshore regions, but can be drawn down by phytoplankton blooms to limiting levels further offshore. Micronutrients other than iron show temporal and spatial variability, although their roles in regulating primary productivity along the WAP are yet to be determined (Bown et al. 2017; Hendry et al. 2008).

1.4. Climate-active gases

1.4.1. Marine carbonate chemistry and air-sea CO_2 fluxes

Carbonate chemistry and air-sea CO_2 fluxes along the WAP are influenced strongly by ocean physics and biological processes. Year-round measurements of dissolved inorganic carbon (DIC) and total alkalinity (TA) taken at the Rothera Time Series since 2010 show that all carbonate chemistry parameters have a strong, asymmetric seasonal cycle in surface waters with some year-to-year variation (Figure 7; Legge et al. 2015, 2017; Jones et al. 2017). Concurrent with the late spring/early summer phytoplankton bloom, DIC, TA and the fugacity of carbon dioxide (fCO_2) decrease sharply, while pH and the saturation state (Ω) of the calcium carbonate minerals calcite and aragonite increase sharply. Values for all parameters then gradually return to winter values. Aragonite saturation state shows notably low wintertime values, just above 1, a critical boundary below which aragonitic organisms can become susceptible to growth impairment and dissolution (Jones et al. 2017). Photosynthesis and respiration dominate these seasonal changes in surface water carbonate chemistry, with biological uptake driving the substantial reductions in DIC during spring and summer (Carrillo et al. 2004; Legge et al. 2017; Tortell et al. 2014). Upwelling and vertical mixing of carbon-rich deep water increase upper ocean DIC, especially during winter, whilst sea ice reduces CO_2 outgassing. Ryder Bay is a net sink for atmospheric CO_2 of 0.90-1.39 mol C m^{-2} yr^{-1} (Legge et al. 2015). It remains unclear whether the WAP shelf as a whole is a net annual sink or source for atmospheric CO_2.

Across the WAP shelf, carbonate system parameters show strong onshore-offshore gradients in the upper ocean during summer, with low DIC and fCO_2 and high pH and aragonite saturation state in near-shore waters, due to strong biological carbon uptake, especially in the southern WAP sub-region (Figure 8) (Carrillo et al. 2004; Hauri et al. 2015; Ruiz-Halpern et al. 2014). The degree of summertime DIC and fCO_2 drawdown is closely related to phytoplankton biomass and primary production (Moreau et al. 2012), which are regulated by winter sea ice coverage and wind patterns during spring (Montes-Hugo et al. 2010). In the central WAP, dilution by meltwater inputs reduces TA and DIC in near-shore waters (Hauri et al. 2015). Most of the WAP shelf exhibited fCO_2 undersaturation and net CO_2 uptake during summers between 2005 and 2009, although there was a region of fCO_2 supersaturation and net CO_2 release in the outer shelf region to the north of Anvers Island (Ruiz-Halpern et al. 2014). Air-sea CO_2 fluxes in Bransfield Strait are highly variable, with surface waters switching between sink and source behaviour in consecutive summer seasons (Ito et al. 2018).

1.4.2. Halogens

Halogen gases can be released from phytoplankton and ice algal communities along the WAP, with consequences for atmospheric chemistry and regional climate. The halogens play an important role in the Antarctic atmospheric boundary layer, being involved in the cycling of O_3, HO_x, NO_x, Hg, CH_4

and the formation of precursor molecules to cloud condensation nuclei (CCN) (reviewed by Saiz-Lopez and von Glasow 2012). Destruction by bromine radicals is thought to be the primary driver for ozone depletion events, during which Antarctic boundary layer O_3 can decrease from around 30 ppb to below instrumental detection (1-2 ppb) for up to a few days (e.g. Jones et al. 2013). Additionally, modelling studies suggest that some halogen oxides are involved in controlling CCN formation through oxidation of the semi-volatile organic sulphur compound dimethyl sulphide by bromine monoxide (Breider et al. 2015) and possibly new particle formation involving iodine oxides (e.g. Saiz-Lopez et al. 2008; Roscoe et al. 2015).

Biotic and abiotic sources of halogens to the Antarctic atmospheric boundary layer have been identified. The 'explosive' emission of bromine needed to initiate ozone depletion events is driven by catalytic liberation from condensed-phase sea-salt bromide present on airborne particulates, and snow and sea ice surfaces (reviewed by von Glasow and Hughes 2015). Sea salt aerosol (Legrand et al. 2016) and blowing saline snow (Yang et al. 2008, 2010; Lieb-Lappen and Obbard 2015) are also thought to be important sources of gaseous inorganic bromine in Antarctica. Whilst these abiotic sources are thought to dominate, Hughes et al. (2009, 2012) show that high rates of biogenic bromoform ($CHBr_3$) flux from diatom blooms in the seasonal ice zone of the WAP could also contribute significantly to gaseous inorganic bromine during certain times of year. Similar to the uptake of macronutrients being reduced during relatively low-productivity spring/summer seasons following winter periods with reduced fast-ice duration (Henley et al. 2017), biogenic bromoform ($CHBr_3$) emissions are also reduced in low-ice low-productivity years (Hughes et al. 2012).

Whilst iodine emissions to the Antarctic atmosphere have also been linked to abiotic reactions on the snowpack (Saiz-Lopez et al. 2008; Freiss et al. 2010), additional biological sources have been proposed for coastal regions at the WAP and elsewhere. These include iodocarbon (e.g. CH_2I_2, CH_3I) emissions from surface waters and sea ice (Chance et al. 2010; Granfors et al. 2013), and microalgal-mediated inorganic iodine flux from sea ice brine channels (Saiz-Lopez et al. 2015).

1.4.3. Organic sulphur compounds

Dimethyl sulphide (DMS) is the most important natural sulphur source to the atmosphere, where it is oxidised to form sulphate aerosols, which act as CCNs and exert a cooling effect through albedo feedbacks. DMS can also be released from phytoplankton and ice algal communities along the WAP, resulting in a direct feedback between the ecosystem and regional climate. Climatologies of DMS concentrations and fluxes show that the Southern Ocean as a whole is a global hotspot of DMS production, and its modelled contribution to atmospheric sulphate is especially high (Gondwe et al. 2003; Lana et al. 2011). The Southern Ocean also exhibits the highest temporal variability in DMS concentrations, and the highest concentrations in the marginal ice zone. The latest Southern Ocean climatology indicates that the WAP is not a particular hotspot of DMS production (Jarníková and Tortell 2016), although this may reflect a shortage of published datasets, particularly from the marginal ice zone. Two time series from the Palmer LTER show highest DMS concentrations in January between 5 and 15 nM (Asher et al. 2017; Herrmann et al. 2012), which compare well with the climatological mean for January of 10.8 ± 6.9 (SD) nM for the whole Austral Polar province (Lana et al. 2011). A recent continuous 5-year time series at Rothera shows large seasonal fluctuations in northern Marguerite Bay, with considerably higher concentrations in January, reaching an average of 24 ± 35 (SD) nM and a maximum of 160 nM in January 2015 (Webb et al. *in review*). This new time series documents a 3-fold higher flux of DMS to the atmosphere than previously calculated. High concentrations were also observed throughout Marguerite Bay and out to the shelf edge in January 2015, and are likely associated with the location of the marginal ice zone (Figure 9; Stefels et al. 2018).

The role of sea ice in the sulphur cycle is complex and the processes involved are poorly quantified. Large phytoplankton blooms and spikes of DMS have been linked to melting sea ice (Trevena and Jones 2006), potentially caused by the release of large amounts of ice algae that produce the DMS precursor, dimethylsulphoniopropionate (DMSP) (Stefels et al. 2018). This is supported by extremely high DMSP concentrations common in sea ice, 2-3 orders of magnitude higher than in underlying surface waters. However, release from sea ice does not necessarily result in high DMS concentrations (Tison et al. 2010). The efficiency of DMSP conversion to DMS depends strongly on phytoplankton community structure, as *Phaeocystis* and dinoflagellates readily convert DMSP into DMS whilst diatoms do not, on bacterial processes, which often demethylate DMSP rather than producing DMS, and on abiotic factors (Stefels et al. 2007). With particular relevance to Antarctic ice and surface waters, high levels of UV radiation can photo-oxidise DMS to dimethylsulphoxide (DMSO), as well as inhibiting algal and bacterial activity (Toole and Siegel 2004; Zemmelink et al. 2008a). Whilst high DMS fluxes have been found above sea ice, it remains unclear how much is derived from surface ice communities, which are often dominated by the well-known DMS producer *Phaeocystis*, and/or from leads between ice floes, where surface-microlayer concentrations of DMS can be an order of magnitude higher than in the underlying water column (Zemmelink et al. 2008a, b). Ice-derived DMS fluxes are likely to be largest during early spring, when surface ice communities are developing and surface ice and snow layers become permeable due to rising temperatures. Sea ice dynamics also impact on pelagic DMSP production, both directly via DMSP release from ice algae input to surface waters, and indirectly by shaping the conditions for pelagic blooms that produce DMSP (Stefels et al. 2018; Webb et al. *in review*).

1.5. Microbial processes

Bacterioplankton (free-floating and particle-attached archaea and bacteria) community dynamics are closely coupled to phytoplankton dynamics in the upper ocean, and strongly influenced by environmental characteristics, such as sea ice, salinity, temperature, stratification and nutrient availability (e.g. Ghiglione and Murray 2012; Luria et al. 2016, 2017; Piquet et al. 2011; Rozema et al. 2017b; Signori et al. 2014; Obryk et al. 2016). These microbial communities play a key role in biogeochemical cycling. Close coupling between bacterial and phytoplankton dynamics along the WAP has been emphasised by microbial studies conducted as part of the Palmer LTER (2002-ongoing) and earlier RACER (1987-1989) projects. Variability in abundance and productivity of bacterioplankton is governed largely by the availability of phytoplankton-derived DOM, as terrestrial input of organic carbon is negligible (Ducklow et al. 2012a) – in great contrast to the Arctic. Bacterioplankton abundance varies across the WAP shelf, being higher further south and towards the inshore regions, in broad agreement with phytoplankton distributions (Figure 10). Pronounced temporal variability is evident as abundance increases from winter minima of $2.0 \pm 0.8 \times 10^8$ cells L^{-1} to a maximum of ~$2\text{-}3 \times 10^9$ cells L^{-1} during summers with high phytoplankton biomass (Ducklow et al. 2012a; Evans et al. 2017). Hotspots of bacterial production and abundance do not necessarily overlap, as production per bacterium can vary by up to an order of magnitude between years, in addition to spatial differences (Figure 10). Multi-year and spatially-extensive studies have suggested a low ratio (~4 %) of bacterial to primary production (Ducklow et al. 2012a; Kim and Ducklow 2016), which is unique to the Southern Ocean and the cause remains unknown (Kirchman et al. 2009). Seasonal-scale studies that have addressed phytoplankton bloom dynamics and bacterioplankton diversity simultaneously suggest that time-lagged responses are important in the coupling between phytoplankton and bacteria, leading to increased heterogeneity in the microbial community (Luria et al. 2014; Moreno-Pino et al. 2016; Piquet et al. 2011; Rozema et al. 2017b; Bowman et al. 2017; Bowman et al. 2016). A stronger relationship between summertime bacterial production and phytoplankton biomass estimated from chlorophyll than with primary production rates suggests that bacteria preferentially utilise DOM derived from grazing, sloppy feeding and viral lysis, rather than DOM excreted by phytoplankton (Ducklow et al. 2012a; Kim and Ducklow 2016; Ruiz-Halpern et al.

2011). Bacterioplankton itself could be an underestimated source of DOM through grazing by zooplankton and mixotrophic algae, or by viral lysis; an important loss factor for Antarctic bacterioplankton (Brum et al. 2015; Evans et al. 2017; Evans and Brussaard 2012; Vaqué et al. 2017). Although studies of DOM origin, speciation and bioavailability are rare in this region, one winter survey revealed that ~35 % of dissolved amino acids, and thus potentially a large proportion of the DOM pool, was of bacterial origin (Shen et al. 2017).

Whilst low *in situ* temperatures could be co-limiting bacterial production along the WAP (Pomeroy and Wiebe 2001), no significant relationship between bacterial production and temperature was observed for half of the summers since 2002, and for the other summers, only weakly-to-moderately significant relationships were found over seasonal timescales (Kim and Ducklow 2016). Temperature may affect bacterial production indirectly, due to its influence on phytoplankton production, grazer activity and diversity, and viral infection (Ducklow et al. 2012b; Kim and Ducklow 2016; Maat et al. 2017; Vaqué et al. 2017).

Stark contrasts exist between surface and deep (>100 m) community composition along the WAP, with diversity being more stable over time and space at depth than in surface waters (Luria et al. 2014). Metabolic structure also varies seasonally and with depth, and can be used to segment bacterioplankton communities along the WAP (Bowman and Ducklow 2015; Bowman et al. 2017). Microbial communities can be transported by ocean currents and winds, increasing connectivity amongst populations (Bowman and Deming 2017; Wilkins et al. 2013). As in the wider Southern Ocean, the dominant phyla are Alpha- and Gamma- Proteobacteria, Actinobacteria and Bacteroidetes (the Cytophaga-Flavobacterium-Bacteroides group) (Abell and Bowman 2005; Delmont et al. 2014; Gentile et al. 2006; Landa et al. 2016).

The pelagic archaeal community along the WAP is dominated by ammonia-oxidising *Thaumarchaeota* (previously Marine Group I *Crenarchaeota*) (Abele et al. 2017; Grzymski et al. 2012; Hernández et al. 2015; Luria et al. 2014; Signori et al. 2014). *Thaumarchaeota* were also found to dominate sea ice and benthic archaeal communities (Cowie et al. 2011; Learman et al. 2016). The widespread distribution of *Thaumarchaeota* suggests an important ecological function involved in nitrogen recycling (Tolar et al. 2016), particularly in winter when bacterioplankton communities are enriched in archaea compared with summer communities (Church et al. 2003; Grzymski et al. 2012; Hernández et al. 2015; Murray et al. 1998; Murray and Grzymski 2007), and nitrogen recycling pathways have been identified in proteomic data (Williams et al. 2012).

High functional diversity is suggested by studies of species composition using the 16S rRNA gene, and confirmed by metagenomics and metaproteomics approaches, which provide a mechanistic understanding of the microbial processes at work. Bacterioplankton are involved in chemoheterotrophy, photoheterotrophy or aerobic anoxygenic photosynthesis during summer, whilst chemolithoautotrophic pathways dominate during winter (Grzymski et al. 2012; Williams et al. 2012). Abundant Flavobacteria have been shown to bind and exploit polymeric substrates, including carbohydrates, polypeptides, and lipids, thereby providing a crucial function in microbial decomposition (Williams et al. 2013). 16S rRNA sequencing data from King George Island have also revealed a previously unknown clade of Archaea potentially capable of oxidising ferrous iron (Abele et al. 2017; Hernández et al. 2015).

1.6. Zooplankton dynamics

Zooplankton abundance, distribution and species assemblages along the WAP are influenced strongly by the availability and composition of their phytoplankton food source, as well as the physical structure of the water column, and play a pivotal role in food web interactions and carbon

593 and nutrient cycling. The major taxa comprising meso- and macrozooplankton (>200 μm, hereafter
594 macrozooplankton) assemblage composition along the WAP are well known, with the Antarctic krill,
595 *Euphausia superba*, being well-established as a keystone species in the regional food web (e.g.
596 Quetin and Ross 2003). The WAP is an important spawning and nursery area for *E. superba*, where
597 spawning success, larval survival over winter and recruitment the following summer are largely
598 dependent on winter sea ice coverage through provision of the ice algal food source and by setting
599 favourable conditions for summer phytoplankton blooms (Atkinson et al. 2004; Saba et al. 2014).
600 Krill spawning and recruitment along the WAP plays a key role in supporting large krill biomass
601 across the southwest Atlantic (Atkinson et al. 2004). The important roles of other taxa, such as the
602 salp *Salpa thompsoni* and the pteropod *Limacina helicina*, in WAP food web dynamics and
603 biogeochemical cycling are increasingly being recognised (e.g. Bernard et al. 2012). In Potter Cove,
604 South Shetland Islands, inshore macrozooplankton assemblages are numerically dominated by the
605 small copepod *Oithona similis*, whereas large copepods such as *Rhincalanus gigas* and *Calanus*
606 *propinquus* tend to dominate in terms of biomass (Garcia et al. 2016).

607 WAP microzooplankton (<200 μm) assemblages are dominated by aloricate ciliates and athecate
608 dinoflagellates (Calbet et al. 2005; Garzio and Steinberg 2013), with tintinnids associated with sea ice
609 (Alder and Boltovskoy 1991). In summer, aloricate ciliate and tintinnid biomass increases with
610 increasing latitude, with high microzooplankton biomass hot spots in productive inner-shelf areas to
611 the south, such as Marguerite Bay (Garzio and Steinberg 2013). Microzooplankton biomass is
612 positively correlated with chlorophyll *a* and particulate organic carbon (POC) concentrations (Garzio
613 and Steinberg 2013).

614 Consistent with most ocean regions, microzooplankton are the dominant grazers during summer,
615 consuming 55-85 % of primary production per day, whilst macrozooplankton (copepods, krill, salps,
616 pteropods) consume on average ~1 % (Bernard et al. 2012; Garzio et al. 2013; Sailley et al. 2013;
617 Gleiber et al. 2015). However, aggregations of krill, salps or copepods common in the WAP result in
618 higher localized macrozooplankton grazing contributions (Bernard et al. 2012; Gleiber et al. 2015). In
619 summer, the impact of macrozooplankton grazing on phytoplankton increases significantly when
620 salps are present, due to high ingestion rates (Bernard et al. 2012). Krill and pteropods are the major
621 macrozooplankton grazers near the coast and over the shelf, whilst salps dominate in offshore slope
622 waters (Bernard et al. 2012). Ingestion rates of copepods in summer are up to 70 times greater in
623 productive coastal waters than offshore (Gleiber et al. 2015). Daily phytoplankton carbon rations for
624 WAP macrozooplankton are often similar to, or even below, those needed to satisfy their metabolic
625 needs and fuel reproduction, indicating that protozoans and other zooplankton are an important
626 food source even during the productive summer period (Bernard et al. 2012; Gleiber et al. 2015).
627 Macrozooplankton have been shown to feed on smaller zooplankton prey in the WAP (e.g. Atkinson
628 and Snyder 1997; Calbet et al. 2006; Atkinson et al. 2012), although potential trophic cascades that
629 could result have not been investigated. There are also regional differences in zooplankton prey
630 quality that could affect top predators, indicated by lower lipid content of *E. superba* in the central
631 WAP compared to the southern sub-region (Ruck et al. 2014).

632 A year-round time-series sediment trap located over the WAP shelf indicates that zooplankton fecal
633 pellets (mostly from krill) dominate export, comprising on average 67 % of the total POC flux over
634 170 m (Gleiber et al. 2012). By comparing copepod fecal pellet flux from the same sediment trap and
635 copepod egestion rates from experiments, Gleiber et al. (2015) estimate on average 58 % retention
636 of copepod fecal pellets in the upper 170 m, such that copepod pellets are likely recycled in surface
637 waters to a greater extent than those from krill. *Salpa thompsoni* along the WAP produce large fecal
638 pellets that sink on average 700 m per day, and have defecation rates that can exceed those of krill
639 (Phillips et al. 2009). Changes in zooplankton species composition can therefore have a significant
640 effect on POC fluxes, biogeochemical cycling, benthic food supply and the biological carbon pump

(Gleiber et al. 2012; Steinberg and Landry 2017). *E. superba* is known to forage on the benthos, which has further implications for benthic-pelagic coupling, including the vertical transfer of particulate iron ingested at depth into surface waters where it is subsequently metabolised and made bioavailable to phytoplankton (Schmidt et al. 2011; Schmidt et al. 2016).

1.7. Higher trophic levels

The WAP ecosystem comprises diverse assemblages and high biomass of top predators that represent both Antarctic and sub-Antarctic habitats, supported by the large and persistent biomass of krill predominantly in the central and southern WAP and the pack ice zone (Costa and Crocker 1996; Ducklow et al. 2007; Friedlaender et al. 2011; Kock and Shimadzu 1994; Nowacek et al. 2011). Along the northern slope and in oceanic waters where copepods dominate, mesopelagic fish and squid act as intermediate consumers. Predator hotspots develop in areas where bathymetric troughs facilitate intrusions of nutrient-rich CDW onto the continental shelf (Dinniman et al. 2011; Friedlaender et al. 2011; Friedlaender et al. 2006; Kavanaugh et al. 2015). More ephemeral predator hotspots are found along fronts and filaments that aggregate and concentrate prey (Bost et al. 2009; Cotté et al. 2015; Dragon et al. 2010; Scheffer et al. 2010; Warren et al. 2009). The biophysical coupling by which predators use and rely on mesoscale features that can aggregate their prey, and the dive behaviours that determine the decisions predators make in response to prey availability (Friedlaender et al. 2016), are critical to how top predators partition their habitat.

While top predators exist in similar regions and often share the same prey, they have different life history patterns and habitat preferences that likely alleviate some of the potential for competition. During the summer, penguins, flying seabirds and fur seals forage along the shelf break and the southern boundary of the ACC, periodically returning to their breeding colonies (Ribic et al. 2011). In winter, seabirds are found near the ice edge, along the shelf break and around the Polar Front to the north (Chapman et al. 2004). While gentoo penguins (*Pygoscelis papua)* remain near their breeding colonies throughout the year (Cimino et al. 2016; Miller et al. 2009), Adélie (*P. adeliae)* and chinstrap (*P. antarcticus)* penguins move far away from their colonies in winter, with Adélie penguins preferring winter sea ice, and chinstrap penguins preferring open water (Hinke et al. 2015; Trivelpiece et al. 2007). Adélie penguins forage in shallow (<200 m) waters near land and in deeper waters (200–500 m) near the edge of deep troughs cross-cutting the shelf (Erdmann et al. 2011). Crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*) and leopard (*Hydrurga leptonyx*) seals remain in the WAP year-round, maintaining access to ice or land to haul out and reproduce (Figure 11) (Costa et al. 2010). While Weddell seals remain in the fjords, crabeater seals move extensively along the shelf, staying closer to the coast in regions with greatest change in bathymetry, and deep within the pack ice throughout the winter (Burns et al. 2004). The short breeding season of southern elephant seals (*Mirounga leonina*) enables them to spend months at sea moving into the pack ice, along the outer shelf and offshore into pelagic waters (Costa et al. 2010). Seals partition their habitat by foraging depth and duration, with the longest and deepest dives by elephant seals (Hindell et al. 2016). Fur seals (*Arctocephalus gazella*) show significant seasonal variability in their distribution, remaining within a few hundred kilometres of their breeding colonies during summer and dispersing widely during winter (Figure 11). Humpback whales (*Megaptera novaeangliae*) forage broadly across the WAP shelf during summer, moving inshore in autumn, with their density and distribution controlled by those of their krill prey and their preference for ice-free conditions and dense aggregations of larger, older krill (Friedlaender et al. 2006; Johnston et al. 2012; Murphy et al. 2007; Weinstein and Friedlaender 2017; Weinstein et al. 2017). Humpback whales forage in a manner consistent with optimal foraging theory to maximize their energetic gains (Friedlaender et al. 2013; Friedlaender et al. 2016; Tyson et al. 2016) and remain in significant numbers in ice-free areas until the beginning of winter. Minke whales (*Balaenoptera bonaernsis*) avoid competition with humpback whales by foraging on deeper krill

689 aggregations (Friedlaender et al. 2009) and, being smaller and more manoeuvrable, they can forage
690 under the ice, their preferred habitat (Friedlaender et al. 2014). Recent work found long-term
691 preferences of minke whales for ice edge regions during summer (Williams et al. 2014) and
692 throughout the foraging season (Lee et al. 2017). While they are known to be the only endemic
693 cetacean species, present year-round, evidence suggests that some portion of the population
694 migrates to sub-tropical latitudes in winter (Lee et al. 2017). Blue (*Balaenoptera musculus)* and right
695 (*Eubalena glacialis*) whales are also seasonally present and similarly feed on krill. Different ecotypes
696 of killer whales (*Orcinus orca*) are seasonally present in the WAP following the distribution of their
697 prey (e.g. seals, whales or fish) (Pitman and Ensor 2003).

698 As well as providing top-down control on the ecosystem, top predators can also influence
699 biogeochemical cycling by transporting macro- and micronutrients vertically and horizontally
700 (Doughty et al. 2016; Ratnarajah et al. 2016; Roman et al. 2014).

701 1.8. Benthic ecosystems

702 Benthic organisms and processes play a critical role in whole-ecosystem structure and functioning
703 along the WAP, as well as biogeochemical cycling and sequestration of carbon from the overlying
704 water column. WAP benthic ecosystems are characterised by a rich diversity of macro- and
705 megafauna including echinoderms such as brittle stars, holothurians, sea urchins, asteroids and
706 crinoids, as well as abundant sponges, ascidians, polychaetes, bivalves, gastropods, brachiopods,
707 bryozoans and sipunculan worms (e.g. Clarke et al. 2007; Gutt 2007; Peck 2018; Piepenburg et al.
708 2002; Sahade et al. 1998; Smith et al. 2012). Hard-substrate communities are widespread in the
709 region around Palmer Station and further north to the South Shetland Islands, and are dominated by
710 large perennial brown macroalgae in shallow waters, with red macroalgae dominating the
711 understory (Wiencke and Amsler 2012; Deregibus et al. 2016; Ducklow et al. 2013). These
712 macroalgae and their epiphytes form important year-round carbon sources in coastal and near-
713 shore systems (Dunton, 2001; Gillies et al. 2012; Jacob et al. 2006; Pasotti et al. 2015), and support
714 rich assemblages of benthic invertebrates, including amphipods, gastropods and echinoderms
715 (Huang et al. 2007; White et al. 2012). South of the Palmer Station region, benthic communities at
716 depths >50 m are dominated by sessile invertebrates including sponges, soft corals, bryozoans and
717 tunicates (Ducklow et al., 2013), whilst mobile scavengers such as starfish, brittle stars and urchins
718 are abundant in shallower waters (Clarke and Johnston 2003). Fjordic systems along the WAP have
719 been shown to exhibit higher abundance and diversity than adjacent shelf areas (Grange and Smith
720 2013).

721 In general, benthic organisms in the WAP region are characterised by very slow growth and
722 development rates, which are slowed beyond the expected effects of low temperature compared to
723 temperate and tropical species (Figure 12) (Peck 2016, 2018). Rates of activity and other processes
724 including routine oxygen consumption are not similarly slowed, indicating that the limitations on
725 growth and development are likely caused by restricted protein manufacture at low temperatures
726 (Fraser et al. 2004, 2007; Peck 2016). The slow growth rates result in extended longevity and
727 deferred maturity (longer generation times), which has been demonstrated in amphipods (Johnson
728 et al. 2001), the bivalve *Adacnara nitens* (Higgs et al. 2009), and a range of other molluscs,
729 brachiopods and echinoderms (Peck 2018). High-latitude Southern Ocean benthic organisms, such as
730 fish (Leis et al. 2013), hyppolytid shrimps (Clarke 1985) and several starfish (Bosch and Pearse 1990),
731 also produce fewer larger eggs, with egg diameters generally 2-5 times greater than those of lower-
732 latitude species (Arntz et al. 1994; Peck 2018).

733 Benthic organisms assimilate carbon fixed by primary producers in the overlying water column
734 and/or sea ice, and can store carbon more efficiently and over longer periods than pelagic organisms

(Barnes 2017; Peck et al. 2010). The degree and timescale of carbon sequestration is dependent on sea ice dynamics and the duration of the ice algal and phytoplankton blooms, local oceanographic conditions such as current speeds and nutrient supply, organisms' lifespans and behaviours, and the frequency of ice scour, which has a major role in structuring shallow benthic ecosystems (Barnes et al. 2018). The contribution of benthic processes to pelagic productivity via nutrient supply at the WAP is a current area of debate. Nutrient release from sediments and porewaters by diffusion, physical disturbance and bioturbation by burrowing organisms, such as polychaetes, echinoderms and bivalve molluscs (Poigner et al. 2013), has the potential to act as a significant source of nutrients to water column biota. Physical disturbance by iceberg scour can expose buried sediments from water depths exceeding 300 m, and can produce sediment scours over 10 m deep (Lien et al. 1989), releasing large quantities of sediment-derived nutrients. Currents entrained by moving icebergs can redistribute sediment several metres up into the water column for short periods and across many metres of the seabed (Bigg 2016; Peck et al. 2005). Icebergs can also distribute sediments over considerable distances and through the water column as ice melts, and act as a dispersal mechanism for some benthic species (Peck 2018). Mixing of the upper water column by icebergs, winds and currents will regulate the extent to which sediment-derived nutrients reach the surface ocean and influence pelagic primary productivity.

2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-climate feedbacks on the changes underway?

Our knowledge of the key mechanisms and interactions regulating ecosystem functioning and ocean-atmosphere coupling along the WAP shelf, and in particular the interdependence between physical, biogeochemical and biological processes, paves the way for understanding the ongoing changes in ice dynamics, ocean physics, biogeochemistry, air-sea exchange, and pelagic, benthic and microbial food webs.

2.1. Physical oceanography and ice dynamics

The long-term change in atmospheric and oceanic properties along the WAP has been a strong focus of scientific efforts given its large magnitude, and its observed and potential impact on the regional ecosystem (Constable et al. 2014a, b; Ducklow et al. 2013; Martinson et al. 2008; Meredith et al. 2017; Schofield et al. 2017; Venables et al. 2013). The evolution of sea ice cover on timescales from seasonal to inter-decadal is a key modulator of physical and biogeochemical processes on the shelf. For example, sea ice extent and its growth and retreat modulate vertical mixing, air-sea fluxes, light penetration, and the salt and heat content of the surface ocean. On average, sea ice extent in the WAP region varies between 1 and 6 x 10^5 km^2 over the annual cycle (Meredith et al. 2017). Alongside substantial warming of the atmosphere and ocean, the period of seasonal sea ice cover has shortened by more than three months since the late 1970s, with autumn advance being delayed by two months and spring retreat occurring more than one month earlier (Stammerjohn et al. 2012; Stammerjohn et al. 2008a). Strong correspondence between retreat and subsequent advance suggests a strong feedback in ocean thermal properties in autumn in response to changes in the timing of retreat in spring. The trend is less clear in the northern WAP (Schloss et al. 2012) where substantial sea ice declines have already occurred, although Bers et al. (2013) showed the strong effect of climatic forcing even in inshore waters of King George Island.

The warming trends and salinity changes documented in the surface and deep water layers across much of the WAP shelf have not been observed in Bransfield Strait, likely because of the modulation by Weddell Sea inflow around the northern tip of the Peninsula (Bers et al. 2013; Meredith and King

2005; Schloss et al. 2012; Schmidtko et al. 2014). This highlights strong gradients along the shelf in the processes controlling long-term property trends, as well as the mean properties themselves. The alongshore structure of mid-depth (>100 m) ocean temperature plays a pivotal role in glacier retreat rates along the WAP, with warmer subsurface waters in the southern and central WAP (south of Bransfield Strait) acting as the primary driver of substantial glacial retreat along the adjacent coast (Cook et al. 2016; Padman et al. 2012). In contrast, glaciers along Bransfield Strait terminate in colder Weddell-modulated waters and are retreating at slower rates, with some even advancing. In cases where glaciers in the northern WAP are experiencing high melt rates and retreat, for example at King George Island, atmospheric forcing is thought to be the primary driver (Falk and Sala 2015).

The observation that the long-term trends of atmospheric warming and sea ice declines have plateaued since the late 1990s (Figure 1), with recent increases in sea ice extent and duration recorded in some places (Schofield et al. 2017; Turner et al. 2016), reflects substantial natural internal variability that is likely to have broad-scale impacts on ocean properties and circulation of the WAP shelf. The nature and importance of these interactions superimposed onto the long-term trends is still to be determined. In contrast, there is no evidence for a slow-down or reversal in the trends of oceanic warming over the southern and central WAP shelf, or glacial retreat along much of the WAP coast (Cook et al. 2016).

2.2. Phytoplankton and microbial community dynamics

The documented sea ice declines since the late 1970s have led to overall reductions in phytoplankton biomass, with regional differences along the WAP in the response of phytoplankton dynamics to the climatic and oceanic changes observed (Montes-Hugo et al. 2009). These changes in phytoplankton dynamics are attributed to changes in sea ice and upper ocean conditions, rather than any long-term trend in CDW incursion and/or nutrient supply. Satellite analyses suggest that the shelf sub-region to the north of Anvers Island experienced decadal declines in summer chlorophyll levels between the early 1980s and early 2000s concurrent with declining sea ice extent and duration (Montes-Hugo et al. 2009; Stammerjohn et al. 2008a, b). Low sea ice cover during winter and early spring leads to low chlorophyll in summer due to increased wind-driven mixing and potentially increased cloud cover, and consequently a less favourable light environment for phytoplankton growth (Montes-Hugo et al. 2009; Saba et al. 2014; Venables et al. 2013). In contrast, satellite-derived chlorophyll increased in the central and southern sub-regions over the same period, attributed to longer periods of open water (Montes-Hugo et al. 2009) resulting from the seasonal declines in sea ice (Stammerjohn et al. 2008a, b). However, strong decreases in chlorophyll in the northern sub-region outweighed the increases further south, leading to an overall reduction in phytoplankton biomass along the WAP (Montes-Hugo et al. 2009). More recently, the increase in sea ice duration since the late 2000s has led to higher chlorophyll levels in WAP coastal regions (Schofield et al. 2017).

Coastal time-series data from Potter Cove at King George Island/ Isla 25 de Mayo (Schloss et al. 2012) and Palmer Station at Anvers Island (Schofield et al. 2017) suggest that the observed declines in phytoplankton biomass reversed around 2010. In Potter Cove, chlorophyll concentrations were typically low between 1991 and 2009, with maximum values (~4 mg m^{-3}) during short-lived episodic events, when phytoplankton assemblages were dominated by large diatoms from several genera (*Corethron criophilum, Odontella weissflogii, Eucampia antarctica, Thalassiosira sp., Porosira sp.*) (Schloss et al. 1997). Nutrients were not limiting, and low phytoplankton biomass was attributed to adverse physical conditions, with intense turbulent mixing and sediment-rich meltwater inputs limiting light conditions for phytoplankton growth and preventing bloom formation (Schloss et al. 2002; Kim et al. 2018). A first high-chlorophyll bloom (~14 mg m^{-3}) lasted approximately two weeks in January 2010 and was followed by several subsequent high-chlorophyll seasons, with the same

827 genera present as earlier in the time series (Schloss et al. 2014; Kim et al. 2018). Whilst a
828 combination of low air temperatures, which delayed the melting of the surrounding Fourcade
829 glacier, and low wind intensities can explain the bloom duration in January 2010, different
830 mechanisms are behind increased productivity in more recent years. Experimental work has shown
831 that smaller diatoms (e.g. *Navicula*, *Nitzschia*, etc.) have greater tolerance to low salinities than large
832 diatoms (Hernando et al. 2015), such that the phytoplankton response to glacial meltwater inputs
833 may differ depending on community composition and the timing of inputs relative to bloom
834 progression.

835 Chlorophyll concentrations have also increased since the late 2000s at Palmer Station, ~400
836 kilometres to the south, concurrent with an increase in the number of days of sea ice cover each
837 year and shallower spring/summer mixed layers, which have led to larger phytoplankton blooms
838 dominated primarily by diatoms (Schofield et al. 2017). This is in contrast to much of the duration of
839 the Palmer time series, where a statistically significant decline in sea ice duration was observed. At
840 the Rothera Time Series (RaTS) in northern Marguerite Bay, ~400 kilometres south of Palmer Station,
841 short-lived winter sea ice cover led to a substantial reduction in summertime chlorophyll levels
842 between 2007 and 2010 (Venables et al. 2013). Since 2010, sea ice duration and chlorophyll have
843 increased again, with sea ice persisting into December and large phytoplankton blooms (chlorophyll
844 >15 mg m^{-3}) in the most recent years. A recent synthesis of chlorophyll and physical oceanographic
845 time-series data from Potter Cove, Palmer and Rothera demonstrates that whilst large-scale climate
846 forcing influences all three sites, local processes such as ice melt and mixing superpose distinct
847 interannual patterns and trends (Kim et al. 2018). Longer-term changes in primary production and
848 community structure over the WAP shelf will depend on the interaction of long-term climatic
849 warming trends and large natural internal variability in regulating seasonal sea ice dynamics over
850 interannual-to-decadal timescales.

851 Projected increases in glacial meltwater input (Meredith et al. 2010) are likely to modify
852 phytoplankton dynamics by promoting upper ocean stability and altering nutrient availability.
853 Combined with long-term reductions in sea ice cover and persistence of deeper mixed layers,
854 increased surface stratification would potentially favour cryptophytes and smaller diatoms over
855 larger diatoms, with shifting phytoplankton community structure as a result (Moline et al. 2004;
856 Schofield et al. 2017).

857 There has been significantly less focus on the consequences of sea ice and physical oceanographic
858 changes for the direct coupling between sea ice and pelagic ecosystems, through ice-ocean
859 exchange and sea ice algal inputs to the water column. Changes in the timing of sea ice retreat may
860 lead to phenological changes, and earlier or later ice algal and/or phytoplankton blooms may result
861 in trophic mismatches as pelagic herbivores become less able to synchronise with the blooms, with
862 negative reproductive consequences and the potential for cascading effects through the entire food
863 web (e.g. Søreide et al. 2010).

864 Relatively little is known about the response of microbial communities to ongoing changes in the
865 physical environment and phytoplankton dynamics. However, response time to changing
866 environmental conditions is known to vary spatially and between phytoplankton and
867 bacterioplankton (Moreno-Pino et al. 2016; Rozema et al. 2017b), likely increasing spatial patchiness
868 in the microbial community (Figure 10) and functional diversity, thus affecting ecosystem resilience.
869 The strong dependence of microbial processes on other rapidly changing ecosystem components,
870 e.g. phytoplankton (Bertrand et al. 2015), zooplankton, benthic organisms, seeding from
871 macrofaunal microbiomes (Bik et al. 2016) or terrestrial systems (Cavicchioli 2015), and the
872 bioavailability of DOM substrate, suggests that continual and pronounced changes in microbial
873 community composition and functioning are likely.

2.3. Biogeochemical changes and air-sea exchange

Physical and biological changes along the WAP are closely related to changes in ocean chemistry and biogeochemistry, in particular the budgets and cycling of macro- and micronutrients, and the production and air-sea exchange of climate-active gases, with the potential for larger-scale consequences and feedbacks. For example, continued glacial retreat can be expected to increase the supply of iron and other micronutrients (Zn, Cd, Co etc.) from glacial and shallow sediment sources, and potentially their availability to phytoplankton (Annett et al. 2015; Annett et al. 2017; Bown et al. 2017, 2018; Hendry et al. 2008; Monien et al. 2017). Seasonal biological uptake of nutrients and carbon will be determined by the documented variability and ongoing changes in seasonal phytoplankton dynamics driven by changes in sea ice and upper ocean conditions (Henley et al. 2017; Legge et al. 2015; Kim et al. 2016).

Changes in the properties, transport and circulation of CDW across the shelf, particularly in the southern and central WAP regions to the south of Bransfield Strait (Martinson et al. 2008; Schmidtko et al. 2014), are likely to increase the supply of macronutrients and CO_2 to subsurface shelf waters. The extent to which this affects surface ocean nutrient and carbon budgets will depend on the evolution of mixing processes in response to sea ice and atmospheric forcing. Carbonate system parameters (DIC, TA, pCO_2) on the Palmer LTER grid do not show statistically significant trends during summer seasons between 1993 and 2012 (Hauri et al. 2015). However, a continuation of the long-term reduction in seasonal sea ice cover and continued strengthening and southward shifting of westerly winds (Le Quéré et al. 2007; Stammerjohn et al. 2008b; Landschützer et al. 2015) may increase upwelling of DIC-rich water and CO_2 outgassing in winter, as well as altering the phytoplankton community and potentially reducing biological CO_2 uptake in summer (Legge et al. 2015; Saba et al. 2014). The resultant reduction in net annual CO_2 uptake along the WAP is unlikely, in itself, to make a significant difference to the functioning of the Southern Ocean CO_2 sink, due to the small size of the WAP shelf region. However, if the changes anticipated at the WAP are manifest across larger areas of the Southern Ocean in the coming decades, the detailed knowledge of the physical and biological mechanisms regulating CO_2 fluxes obtained in the WAP system will be useful in projecting change at the wider scale, which could be significant terms in the global carbon budget.

Given that sea-to-air emissions of halogens and DMS are directly linked to sea ice dynamics (von Glasow and Hughes 2015) or are derived from the ecosystems that exist within or around sea ice (Hughes et al. 2013; Stefels et al. 2018), it is likely that the sea ice changes and variability observed along the WAP in recent decades will alter the fluxes of these gases to the atmosphere over interannual and longer timescales. This will be important for climate (through aerosol and CCN formation) and atmospheric chemistry (via tropospheric ozone destruction) locally and regionally.

2.4. The WAP pelagic food web

Interannual variability in phytoplankton biomass has strong implications for the productivity of the entire food web, with low chlorophyll years leading to less successful recruitment of the keystone species Antarctic krill *(Euphausia superba)* (Atkinson et al. 2004; Saba et al. 2014). As such, low sea ice conditions are likely to hold negative consequences for higher trophic levels such as penguins, flying sea birds, seals and whales (Constable et al. 2014a, b; Costa et al. 2010; Trivelpiece et al. 2011). Conversely, the recent increases in chlorophyll are likely to be beneficial for zooplankton and their pelagic and benthic consumers (Saba et al. 2014).

Seasonal changes in WAP macrozooplankton abundance are driven by a combination of long-term trends linked to warming and sea ice declines, sub-decadal shifts attributed to oscillations in atmospheric forcing, such as SAM and ENSO, which affect sea ice dynamics and sea surface

919 temperature, and local and regional changes in primary production, all of which have strong
920 interdependences (Figure 13; Steinberg et al. 2015). For example, a decrease in krill density between
921 the 1970s and early 2000s in the WAP and southwest Atlantic sector of the Southern Ocean was
922 attributed to long-term warming and sea ice declines, which reduce the availability of the winter and
923 spring ice algal food source required to promote larval survival and recruitment, as well as driving
924 the overall decline in the summer phytoplankton food source (Atkinson et al. 2004; Montes-Hugo et
925 al. 2009). It has been contested that this decline in krill resulted from a period in the decadal-scale
926 population variability of unusually high krill abundance in the late 1970s, rather than being driven by
927 climate change over subsequent decades (Loeb and Santora 2015). However, more recent evidence
928 has shown a southward contraction of krill distribution throughout the sector over the last 90 years,
929 with a concomitant reduction in juvenile recruitment linked to reduced food availability, and a
930 concentration of the population over the WAP shelf (Atkinson et al. 2019). Since the early 1990s, krill
931 abundance on the Palmer LTER grid (central and southern WAP) has shown a stable 5-year cycle that
932 reflects variability in reproductive and recruitment success linked to ENSO cycles and their influence
933 on sea ice dynamics (Loeb et al. 2009; Quetin and Ross 2003; Ross et al. 2014; Steinberg et al. 2015),
934 in broad agreement with findings from the northern WAP around the South Shetland Islands (Loeb
935 and Santora 2015; Richerson et al. 2017). Accordingly, both *E. superba* and *Thysanoessa macrura* are
936 positively correlated to regional primary production two years prior (Figure 13; Steinberg et al.
937 2015). Local effects can also be pronounced, for instance high krill mortality in Potter Cove in recent
938 years is attributed to unfavourable conditions caused by high meltwater-sourced particle loads from
939 a retreating glacier (Fuentes et al. 2016). In contrast to krill, abundance of the major copepod taxa
940 showed a regional long-term increase over the shelf between 1993 and 2013 (Gleiber 2015).
941 Variability in *Salpa thompsoni* over the shelf is influenced by both ENSO (Loeb and Santora 2012) and
942 SAM (Figure 13; Steinberg et al. 2015), whilst long-term increases throughout the southwest Atlantic
943 sector have accompanied the declines in krill (Atkinson et al. 2004). Variability in abundance of the
944 pteropod *Limacina helicina* along the WAP is also linked to ENSO cycles (Figure 13; Loeb et al. 2009;
945 Loeb and Santora 2013; Ross et al. 2014; Steinberg et al. 2015). Shifts in phytoplankton community
946 structure can also affect the abundance of krill relative to other major zooplankton taxa, because the
947 grazing efficiency of *E. superba* is reduced significantly on particles <20 µm, such that diatom-
948 dominated communities are likely to favour krill, whilst communities dominated by cryptophytes
949 and/or haptophytes are likely to favour salps and other taxa (Haberman et al. 2003; Meyer and El-
950 Sayed 1983; Moline et al. 2004). Shifts in the dominance of krill compared to other taxa have major
951 consequences for higher trophic levels that rely on krill as their primary food source, as well as for
952 carbon export and nutrient recycling, and may lead to substantial reorganisations of the pelagic food
953 web (e.g. Atkinson et al. 2004, 2019; Quetin and Ross 2003).

954 The distribution and abundance of a number of krill-dependent pelagic consumers are changing in
955 concert with changes in the physical environment and the availability of krill (Constable et al. 2014a,
956 b). Winter sea ice conditions along the WAP are particularly important for krill predators, because
957 they regulate krill availability and therefore foraging conditions, which are a key determinant of
958 recruitment and overwinter survival of adult and juvenile animals (Hinke et al. 2017b). Sea ice-driven
959 changes in phenology can also lead to trophic mismatches between predator foraging needs and
960 prey availability, with major demographic consequences (Youngflesh et al. 2017). Populations of ice-
961 dependent Adélie and chinstrap penguins have declined significantly (e.g. Figure 14; Ducklow et al.
962 2013; Hinke et al. 2017a; Juares et al. 2015; Trivelpiece et al. 2011) and the only Emperor penguin
963 colony at the WAP has been lost due to changes in seasonal sea ice duration (Trathan et al. 2011).
964 Southward shifts of the maritime climate, displacing the Antarctic climate, have also increased
965 precipitation and snow accumulation, which reduces the survival of Adélie penguin chicks (Carlini et
966 al. 2009; Chapman et al. 2011). In the northern WAP in particular, the shift to a more maritime
967 climate is likely to shift southward the distributions of ice- and krill-dependent species, such as
968 Weddell and crabeater seals, minke whales and Adélie penguins, leading to local declines as their

habitat contracts with diminishing sea ice (Ducklow et al. 2013; Huckstadt et al. 2012a; Siniff et al. 2008). In contrast, ice-tolerant species such as fur seals, humpback whales and gentoo penguins and those less dependent on krill, such as elephant seals, have increased in number (Costa et al. 2010; Ducklow et al. 2013) and in the length of time they remain feeding locally (e.g. Friedlaender et al. 2016; Weinstein and Friedlaender 2017). The decline in Adélie penguin numbers slowed down in the mid-2000s and the total number of penguins stabilised, although this was a consequence of increasing gentoo penguin numbers (Figure 14). Some krill predators exhibit trophic plasticity and can increase their consumption of fish in years of lower krill availability (e.g. crabeater seals; Huckstadt et al. 2012a), although the extent to which this plasticity can relieve the dependence on krill remains unknown. Sub-Antarctic King penguins (*Aptenodytes patagonicus*) have extended their distribution southwards, recently being recorded for the first time at King George Island (Juares et al. 2017). Increasing westerly wind intensity has benefitted wandering albatrosses (*Diomedea exulans*), by increasing their foraging speeds and reducing trip length, thus enhancing their foraging efficiency and breeding success (Weimerskirch et al. 2012).

2.5. The WAP benthic food web

Benthic communities along the WAP are sensitive to variability in physical and biogeochemical forcing, because many organisms are sessile and therefore unable to migrate. Benthic responses to ocean warming depend on organisms' abilities to adapt or acclimate to altered conditions. Antarctic benthos have a reduced capacity to adapt compared to lower-latitude populations, due to their low production rates of novel genetic material that enhance survival, which arise from longer generation times and production of fewer larger eggs, without an increase in mutation rate or population size (Arntz et al. 1994; Higgs et al. 2009; Johnson et al. 2001; Peck 2018). Geneflow between Antarctic populations is also slower than for temperate or tropical populations due to relatively high levels of protected development and proportionally fewer species using pelagic larval dispersal (Arntz et al. 1994; Peck 2018; Hoffman et al. 2011, 2012). For species that do use pelagic dispersal, rising ocean temperatures increase larval development rates, thus shortening the larval phase substantially (Peck 2016, 2018). This reduces dispersal distances and increases isolation between populations, as well as altering the timings of reproductive cycles in relation to key environmental events (Bowden et al. 2009), such that larval success may decline significantly due to phenological mismatches as warming proceeds.

Given limited rates of adaptation, Antarctic benthos need sufficient phenotypic plasticity to acclimate to altered conditions and survive the projected climate change in coming decades (Peck 2011). Antarctic fish (Bilyk and DeVries 2011) and invertebrates (Morley et al. 2016; Peck 2018; Peck et al. 2009, 2014) have very limited tolerance to warming in laboratory-based experiments, indicating that acclimation to elevated temperature is poor in Antarctic species (Peck et al. 2014). Thermal tolerances are influenced by a number of different species-specific factors (Clark et al. 2017), including heat shock responses to warming (Clark and Peck 2009; Clark et al. 2008), and upper temperature limits being set by accumulation of toxic metabolic end-products (Heise et al. 2007), limitation of energy reserves (Peck 2018; Peck et al. 2014), and temperature sensitivity of critical enzymes (Clark et al. 2016). In general, the rate of oxygen supply to tissues (Pörtner and Farrell 2008; Pörtner et al. 2012) does not appear to exert a major limitation on thermal tolerance (e.g. Devor et al. 2016). The first *in situ* warming experiment in the Southern Ocean, conducted at Rothera Station, showed that growth of biofouling species was significantly faster at 1°C above ambient than at ambient (Figure 15). This was attributed to factors including more efficient protein synthesis and faster processing of food allowing greater nutrient intake in a summer season (Ashton et al. 2017). Mixed results from +2°C treatments likely indicate that growth of some species was restricted by their temperature limits.

Benthic community structure is strongly influenced by ice dynamics along the WAP. Whereas sea ice organic fluxes are an important food source for the benthos, solid ice can have a devastating effect by removing a significant proportion of macro- and meiofauna from the seabed (Peck et al. 1999; Lee et al. 2001). Iceberg impacts can be very frequent in shallow waters along the WAP (Brown et al. 2004), and ongoing increases in iceberg scour driven by glacial retreat, receding ice shelves and an overall decline in fast ice have caused a marked drop in biomass of shallow benthic fauna in Ryder Bay, Adelaide Island (Barnes and Souster 2011). This is expected to continue, and potentially intensify in the coming decades (Barnes 2015; Smale et al. 2008). In Potter Cove, South Shetland Islands, increased sedimentation from a retreating glacier was the most important factor driving sudden shifts in nearby benthic assemblage composition with unexpectedly rapid loss of diversity and biomass (Sahade et al. 2015; Torre et al. 2017). Contrary to the adverse effects of ice scour and ice-derived sedimentation, the retreat of coastal glaciers and disintegration of ice shelves along the WAP has opened up new ocean areas for pelagic productivity and benthic ecosystem development (Peck et al. 2010). The loss of benthic carbon storage caused by increased iceberg scour during glacial retreat and ice shelf disintegration is significantly outweighed by the increase in carbon storage resulting from increased primary production and benthic biomass, such that these ice losses lead to a substantial net increase in carbon drawdown to the seabed (Barnes 2015, 2017; Barnes et al. 2018). Glacial retreat has also opened up newly ice-free areas in Potter Cove, including a new island, which have been colonised by communities exhibiting high diversity, biomass and a complex structure at rates far exceeding previously observed or predicted rates in Antarctic benthos (Lagger et al. 2017a, b). Macroalgal forests can colonise recently ice-free hard substrates (Campana et al. 2018; Quartino et al. 2013), and may expand further in the northern WAP in future as more frequent ice-free winters and early spring fast-ice disintegration are expected to increase the annual light budget (Deregibus et al. 2016). Bacterial groups that dominate in sediments enriched with macroalgal detritus (e.g. Proteobacteria, Bacteroidetes, Planctomycetes and Verrucomicrobia) would also become increasingly important with continued macroalgal expansion (Abele et al. 2017; Pasotti et al. 2015). The net effect of ongoing ice changes for benthic communities along the WAP will depend on water depth and proximity to glaciers and/or ice shelves, and their effect on iceberg scour, sedimentation and light availability. Results from Potter Cove show that benthic ecosystem responses may be non-linear and particularly rapid, intense and heterogeneous in fjordic systems. Throughout the coastal WAP, longer-term losses of glaciers and ice shelves may reduce ice scour and sedimentation significantly, increasing benthic carbon drawdown substantially, but the timing of these changes is unknown.

Invasive species occur on the WAP shelf as a result of larval dispersal and anthropogenic vectors such as ship ballast water and hull biofouling (Clayton et al. 1997; Hughes and Ashton 2017; Lee and Chown 2009). The long-term warming and sea ice trends are altering the natural barriers to species invasions along the WAP, by dampening the effect of sea ice cover in reducing dispersal and killing potential invasives, by increasing the coverage of year-round ice-free shallow benthic habitats, and by weakening the temperature limitation of biological processes in warmer-water species (McCarthy et al. 2019). These trends combined with increasing ship traffic are likely to promote the import and success of invasives along the WAP, with potential for major ecosystem disruption, although the timing, magnitude and impact of these invasions is not known.

2.6. Ecosystem responses to ocean acidification

Ocean acidification is expected to be particularly pronounced and to occur earlier in the Southern Ocean, which absorbs more than 40 % of global anthropogenic CO_2 (Fletcher et al. 2006; Orr et al. 2001), than in other ocean regions (Feely et al. 2009; McNeil and Matear 2008; Orr et al. 2005). Whilst statistically significant trends in inorganic carbon and pH have not yet been detected at the WAP (Hauri et al. 2015), aragonite Ω close to 1 has recently been documented in the coastal WAP

during winter (Jones et al. 2017), making aragonitic organisms susceptible to small changes in pH. Decadal enrichment in inorganic carbon and acidification have been documented in the Drake Passage to the north (Hauri et al. 2015; Takahashi et al. 2014), suggesting that this mechanism may have significant ecosystem consequences along the WAP in future.

Ocean acidification has the potential to impact on WAP phytoplankton communities, as experiments from the Ross Sea have shown a shift from the small haptophyte *Phaeocystis antarctica* or pennate diatoms at low CO_2 to large centric chain-forming *Chaetoceros* diatoms at elevated CO_2 levels (Tortell et al. 2008; Feng et al. 2010). These findings were supported by laboratory studies that suggest diatoms may have a competitive advantage over other taxa at elevated CO_2 (Chen and Gao 2004; Sobrino et al. 2008; Wu et al. 2010). An acidification-driven shift towards larger diatoms would act against the proposed shift towards smaller diatoms, haptophytes and cryptophytes driven by changing ice distributions and freshwater inputs (e.g. Hernando et al. 2015; Rozema et al. 2017a; Schofield et al. 2017). As such, the phytoplankton response to competing physical and biological forcings along the WAP could vary significantly over time and space, compounding variability in the forcings themselves. Shifts in phytoplankton species composition could have significant consequences throughout the food web due to different feeding preferences of the major zooplankton taxa and their consumers.

The effects of ongoing atmospheric CO_2 uptake and ocean acidification on polar zooplankton are not well understood. To the north of the WAP in the Scotia Sea, live pteropods (*L. helicina*) showed signs of shell dissolution in a region undersaturated with aragonite (Bednaršek et al. 2012). Conversely, recent evidence for *L. helicina* from the Arctic repairing their shells after mechanical and dissolution damage suggests that these pteropods may be more resilient to ocean acidification than previously thought (Peck et al. 2018). *E. superba* in the WAP region have been shown to increase their feeding and excretion rates under high CO_2 conditions, especially in the case of pregnant krill (Saba et al. 2012).

Antarctic benthos are thought to be vulnerable to current and future ocean acidification, because many have calcified skeletons that use up a greater proportion of the organism's energy budget than lower-latitude species (Watson et al. 2017), as well as low physiological rates and a limited ability to resist environmental change in general. Research on the capacity of Antarctic benthos to acclimate to lowered pH is conflicting, with some studies showing poor capacities in certain organisms (e.g. Schram et al. 2016), whilst most studies demonstrate little effect of lowered pH, even on early stages (e.g. Catarino et al. 2012), and several studies demonstrate greater effects of temperature than pH (Byrne et al. 2013; Cross et al. 2015; Kapsenberg and Hofmann 2014). Recent studies show that although long acclimation periods are required, Antarctic benthos can acclimate to altered pH, at least to end-century conditions, and acclimated organisms exhibit physiological and reproductive performance similar to those in controls (Cross et al. 2015; Suckling et al. 2015; Morley et al. 2016).

3. Overarching priorities and approaches for future work

Whilst significant progress has been made in recent decades in understanding the functioning of the WAP shelf ecosystem, its physical and biogeochemical drivers, the coupling between the ocean and atmosphere, and how these interactions are changing over time, critical knowledge gaps remain. Further elucidation is required regarding the relative importance of the different controlling mechanisms and the interactions between these mechanisms, in order to develop a whole-system understanding of the WAP shelf ecosystem and its response to ongoing changes in climate and the physical environment over seasonal-to-decadal timescales. As sea ice dynamics exert such an important control on ocean physics, chemistry and ecosystem functioning, a fundamental challenge for the observational and modelling communities is to unravel the importance of long-term climate-

driven trends compared with large natural internal variability, and consequently the extent to which the recent slow-down in warming and sea ice losses will persist against the background long-term trend. This challenge is a highly active area of research for the international community (Reid and Massom 2015; Reid et al. 2018), but will ultimately require longer time series of satellite and *in situ* ocean and sea ice measurements, and an improvement in the performance of IPCC-class models for the forthcoming Coupled Model Intercomparison Project Phase 6 (CMIP6). Regional models can be used to elucidate the important local-scale ice-ocean-atmosphere feedbacks modulated by relatively small-scale processes (e.g. ocean eddies with scales of a few kilometres). However, given the known dependence of WAP climate on remote processes (e.g. ENSO, and its interaction with the SAM), these models would need to take reliable boundary conditions from global climate/Earth System models that reproduce both the low-latitude modes and their propagation to high latitudes. Such a framework would allow us to increase the reliability of the relevant signals in the IPCC-class models and improve our ability to project future changes in ice coverage and duration.

Table 1 outlines the important discipline-specific research objectives in WAP marine science over the next 2-10 years, and Table 2 outlines the key approaches and innovations required to address these objectives. One of the major findings over the last three decades has been the importance of physical oceanographic processes in modulating biological and biogeochemical processes, from nutrient supply and phytoplankton dynamics to zooplankton distributions and foraging behaviour of pelagic consumers. This degree and multilateral nature of physical control makes defining the processes of oceanic water mass transport onshore, and its modification and vertical ventilation on the shelf, a key priority. The importance of ice-ocean interactions necessitates full characterisation of sea ice dynamics, glacial meltwater and other freshwater inputs, and their modulation of these physical processes. Quantifying these physical dynamics will pave the way for projecting their impacts on biogeochemical and biological processes throughout the entire food web. Pronounced spatial heterogeneity and temporal variability on timescales of several days to decades necessitates longer time series capturing the complete annual cycle and increased temporal and spatial resolution of observations across the shelf, including under the sea ice. This increased resolution and capability can be achieved by developing an observing system for the WAP shelf combining traditional ship- and station-based approaches with novel technologies based on gliders, autonomous underwater vehicles (AUVs), and mooring and high-frequency (HF) radar networks.

HF radar measures ocean surface (upper 1 m) current velocities over hundreds of square miles simultaneously. A shore-based three-site HF radar network deployed recently at the WAP provides hourly surface current data over the entire Palmer Station region (Figure 16), and has been used with penguin foraging data to identify the selection of foraging locations relative to mapped convergent features over the Palmer Deep canyon (Kohut et al. 2014). These systems have proven to be robust and cost-effective with many applications, and a significant opportunity exists to develop a shelf-wide integrated system to define the regional surface ocean circulation, which is currently one of the least understood aspects of the shelf circulation.

Moorings have been deployed routinely along the WAP, providing high-frequency time-series measurements year-round for over a decade. These moorings have been critical in documenting the frequency and mechanisms of subsurface intrusions of modified CDW onto the continental shelf (Martinson and McKee 2012; Moffat et al. 2009). A key limitation of moorings is that they are typically unable to collect data near the surface, due to the presence of seasonal ice and icebergs (Savidge and Amft 2009), and their spatial coverage is limited.

Autonomous gliders (Sherman et al. 2001; Eriksen et al. 2001; Webb et al. 2001) are complementing mooring measurements by providing high-resolution spatial measurements over the full shelf depth (Carvalho et al. 2016; Carvalho et al. 2017; Couto et al. 2017; Brearley et al. 2017). These gliders are

capable of sampling over thousands of kilometres and spending months at sea, making them ideal for maintaining a sustained presence and filling critical observational gaps between ship-board surveys, research stations and mooring arrays, and at smaller spatial scales than are captured by shipboard sampling (Venables et al. 2017). These systems are cost-effective, capable of carrying a range of physical and biogeochemical sensors, and have been proven to be effective tools to leverage data collection across a broad range of applications and ocean regions (Schofield et al. 2015).

Powered AUVs have been used in the Southern Ocean for bathymetric, physical oceanographic and biological surveys under and in the vicinity of sea ice (e.g. Brierley et al. 2002). Expanding the use of such AUVs in the WAP region has the potential to provide a wealth of water column data from under-ice environments. Most under-ice powered AUV missions to date have been conducted by large complex platforms capable of under-ice navigation and advanced autonomous decision-making, requiring ship support and making deployments expensive. Transitioning to smaller, less complex and less expensive systems capable of sustained missions would increase the number and scope of deployments at the WAP and elsewhere.

Using autonomous technologies will be of particular value in improving observational coverage during ice formation in autumn, the ice-covered winter period and the springtime transition from winter into the ice-free phytoplankton growing season. These times of year are critically important in regulating phytoplankton bloom dynamics, and other key ecosystem processes, yet remain severely undersampled across all disciplines of WAP marine science. In future, real-time sampling and data transfer using these technologies has the potential to inform predictions of key ecosystem processes at the seasonal scale, e.g. phytoplankton bloom timing, magnitude and distribution based on satellite, mooring and profiling float data, with gliders providing measurements/parameterisations of mixed layer depth and stability. Upscaling the use of gliders and powered AUVs in the seasonally ice-covered WAP shelf environment would require a robust and well-integrated system for under-ice navigation, using compact accurate inertial navigation systems and/or acoustic telemetry networks that allow AUVs to triangulate their position. Such systems would facilitate major innovations in future observational studies, for example in elucidating the role of small- and meso-scale processes under the ice, the transports they produce, and their effect on the larger-scale circulation, under-ice ecosystems and biogeochemical cycles. Alongside technological developments in observational approaches, improvements in the resolution of regional ocean circulation models and incorporation of realistic bottom topography are required to fully resolve the most important physical drivers of the shelf ecosystem.

Utilising the WAP shelf region as a natural laboratory or model system to understand the impacts of climate and sea ice changes and the resultant physical oceanographic changes here and in other marginal ice zone settings on phytoplankton dynamics, carbon and nutrient cycling, air-sea fluxes of climate-active gases, and pelagic, benthic and microbial food webs requires an integrated approach. Novel process-based experimental, technological and modelling approaches should be combined with the long-running time-series and spatial measurements that form the backbone of our knowledge of variability and change in the WAP marine system. Given pronounced heterogeneity across the shelf, quantifying the importance of biological hotspots for the regional ecosystem and biogeochemical cycling is a high priority. Detailed process studies and repeat sampling of these hotspots, including along the sea ice edge and in the high-productivity fjords, will improve our understanding of the conditions required to create these hotspots and their change over time.

In such a highly coupled system, it is imperative to cross-cut disciplinary boundaries and characterise the interactions between different system components, e.g. phytoplankton, zooplankton and microbial dynamics in regulating biogeochemical cycling and the biological carbon pump, bottom-up

versus top-down predation control of zooplankton distributions, and benthic faunal composition and behaviours and benthic-pelagic nutrient fluxes. Further application of genomics, transcriptomics and proteomics approaches has the potential to revolutionise our understanding of microbial processes and interactions, and marine ecosystem functioning in general, by revealing vital functions of phytoplankton and bacterioplankton, and identifying the many viruses infecting a range of hosts. Combining a range of methodologies relevant to different processes, interactions and timescales will also be critical to making progress. Adopting such an interdisciplinary whole-system approach offers perhaps the most promising opportunity for driving a step-change in our understanding of the functioning of the WAP marine ecosystem and its response to, and role in, ongoing climatic and environmental changes, making this a clear overarching priority for the international community.

Temporal and spatial coverage of data illuminating these physical-biological-biogeochemical interactions can be augmented by maintaining and strategically enhancing the existing programs of sustained observations, by adopting the essential ocean variables (EOVs; Constable et al. 2016; A Framework for Ocean Observing, 2012) as a framework for an observing system for the WAP, and by employing technological innovations to fill data gaps and increase resolution in time and space. In addition to the discipline-specific approaches and innovations outlined in Table 2 and the physics-based technologies detailed above, a number of sensor-based innovations can be employed across disciplines and provide a more integrated perspective. For example, the utility of AUVs, gliders and moorings can be expanded substantially by increasing the number and reliability of sensors capable of measuring a range of physical, biological and chemical parameters (e.g. turbulence, fluorescence, pCO_2, nitrate). Equipping seals with small CTD tags has provided the extensive hydrographic MEOP (Marine Mammals Exploring the Oceans from Pole to pole) dataset alongside complementary animal behaviour data (Treasure et al. 2017), with significantly greater coverage than otherwise available. Developing and deploying a greater range of sensors (e.g. fluorescence, dissolved oxygen etc.) would facilitate more detailed sampling in ice-covered regions, near-shore embayments and over larger spatial scales than ship-based efforts. Systematic deployment of multi-frequency acoustics on ships, moorings and AUVs would allow us to estimate krill biomass and distribution, and the movement and foraging behaviour of their pelagic predators, with unprecedented accuracy and coverage across the shelf, including in the data-sparse southern region and under ice.

In the context of physical controls on ecosystem structure and functioning, a major question to be addressed is the extent to which organisms at all trophic levels can acclimate, adapt, migrate, and/or change their behaviours, and the rates at which these processes can occur. Process studies and manipulation experiments are required, focusing on the physiological profiles of the major species of phytoplankton, bacterioplankton, viruses, zooplankton and benthic organisms across current and future physical (temperature, salinity, mixing), chemical (macro- and micronutrients, pCO_2 and Ω) and ecological (grazing pressure, viral infection) conditions, and therefore their ability to acclimate. Rates of geneflow within and between populations are needed to quantify the capacity of benthic and pelagic communities to adapt to altered environments. Top predators can be used as sentinels of ecosystem change as their abundance and distributions reflect those of their prey. Reproductive studies targeting major zooplankton taxa and higher trophic level organisms and in-depth studies of the growth, diet and behaviours of juveniles would inform our assessments of recruitment success and population dynamics of key species, and their responses to different conditions. Understanding organisms' abilities to acclimate, adapt, migrate and/or change behaviours, and over what timescales, will shed light on the resilience and sensitivity of different ecosystem components in the face of pronounced environmental variability and change, and their response to multiple natural and anthropogenic stressors.

Direct human pressure on regional krill stocks is increasing as a result of expanding commercial fishing activity, particularly in the northern WAP and adjacent open ocean, potentially reducing food

availability for krill predators (Trivelpiece et al. 2011). Management of this fishery by the Convention on Conservation of Antarctic Marine Living Resources (CCAMLR) must be informed by our knowledge of the foraging behaviour of krill predators, for instance using satellite tags and motion-sensing tags to determine the critical locations and times of year for their feeding (Weinstein et al. 2017), so that any overlap and potential competition with fishing activity can be minimised (Hinke et al. 2017b).

Enhancements of our observational capacity and coverage across the WAP shelf must be accompanied by continued development of modelling frameworks and capabilities to reveal the most important mechanisms behind variability and change at all levels of the ecosystem. Improving the resolution and scope of regional physical, biogeochemical and habitat or ecosystem models is a particular priority, given large heterogeneity spatially and over daily to decadal timescales. Better-constraining the rates of key processes, such as onshelf CDW transport, meltwater inputs, algal growth and organic matter remineralisation, and the major fluxes of heat, nutrients, gases and particles based on coherent high-quality observational data is needed for optimisation of model input parameters and boundary conditions. Ongoing development of regional system models will allow us to test the relative importance of different processes, elucidate the combined and/or competing effects of multiple stressors, and explore the feedbacks between the drivers and consequences of change amongst the different system components over a range of timescales. Further, only once we can represent accurately the key processes and interactions at work in modelling frameworks can we be confident in our projections of future changes in upper ocean mixing, nutrient supply, primary production, ecosystem functioning and resilience, and air-sea exchange of climate-active gases as the changes in sea ice extent, duration and atmospheric forcing continue to evolve. Ultimately, better quantification of the processes and feedbacks at the WAP, and their interactions with systems up- and down-stream in regional atmospheric and oceanic circulation systems, will enable us to better-represent this Southern Ocean region in global climate models and understand its role in contemporary global change.

4. Closing remarks

We have demonstrated the importance of the WAP marine system due to pronounced variability and change in the physical environment and ocean-climate interactions, strong biological and biogeochemical consequences locally and regionally, and its utility as a natural laboratory for examining how climate and sea ice changes might restructure ecosystems here and elsewhere. We have summarised the state of knowledge regarding the key mechanisms and interactions regulating ecosystem functioning and ocean-atmosphere coupling, as well as the changes underway and the ecosystem responses and ocean-climate feedbacks. We also highlight the overarching priorities and discipline-specific objectives for future research and present a vision for an observing system capable of addressing these priorities and objectives. Working towards this vision will require further improvements in integration, collaboration and co-ordination across national programs, projects and initiatives, including sharing of expertise, standardisation of field, experimental and analytical techniques, and optimisation of ship-time, station infrastructure and other resources. To this end, SOOS has recently launched the Due South online database of ship- and station-based fieldwork programs in the Southern Ocean (https://data.aad.gov.au/duesouth/), as well as establishing regional working groups for the WAP and other regions. More effective engagement with other research communities, such as the climate science, meteorology, glaciology, terrestrial biogeochemistry and paleoclimate communities will be critical in defining the most important external controls on the WAP marine environment, the key fluxes into and out of the system, and the longer-term context of the changes underway.

Improvements in data accessibility across disciplines and national programs is also called for, following the examples of the Palmer LTER project (http://pal.lternet.edu/data), the KRILLBASE

database for zooplankton survey data (Atkinson et al. 2017) and the Surface Ocean CO_2 Atlas (Bakker et al. 2016). Widespread adoption of similar data policies and practices across the international community, and efficient linking of existing publicly available databases, for example using the SOOSmap online data portal (http://www.soos.aq/data/soosmap), would be of significant benefit. Co-ordinating and opening up all data sources is recommended as a significant scientific opportunity for the international community working across multiple disciplines in the WAP region and beyond.

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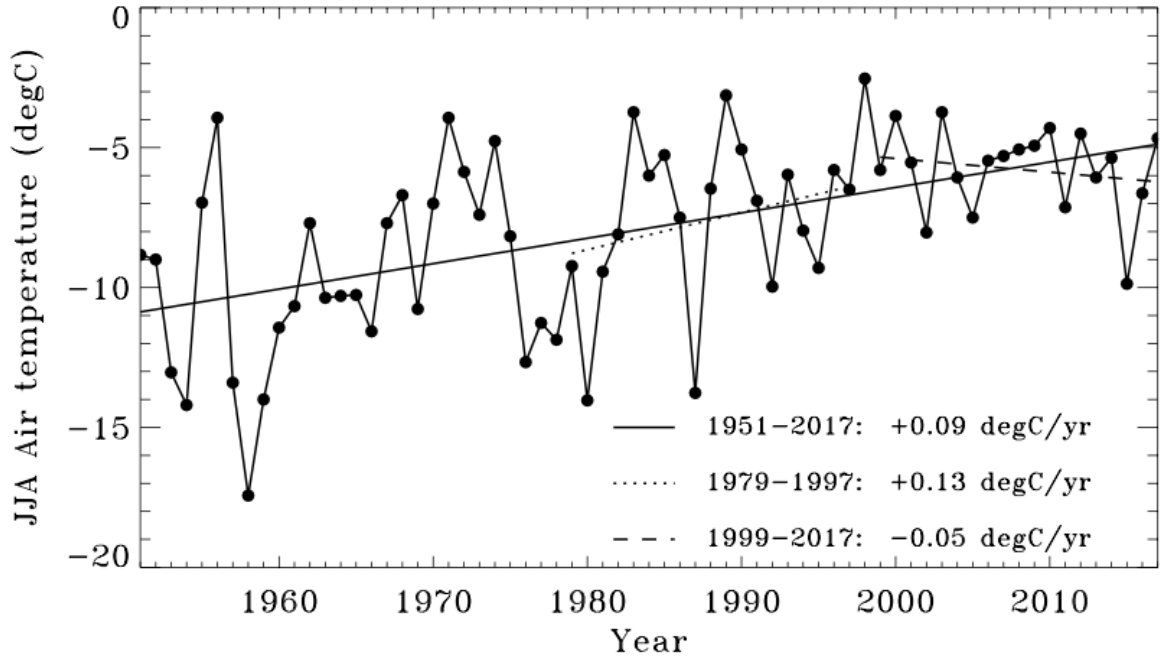
Author contributions: SFH coordinated the project and led the writing of the manuscript. KRH, OMS and MPM instigated and oversaw the project, and contributed substantially to the writing of the manuscript. IRS, DKS, CM, LSP, DPC, DEB, CH, PDR, HWD, DA, JS, MAvL, CPDB, AGJB, JK, RS, ASF, SES and HJV contributed significantly to the writing of the manuscript and the production of figures. All authors have approved the version for submission.

Competing interests: There are no competing interests associated with this work.

Declaration of interests: none

Figures

Note: Figures 2-11 and 13-16 should be published in colour; Figures 1 and 12 should be black and white.



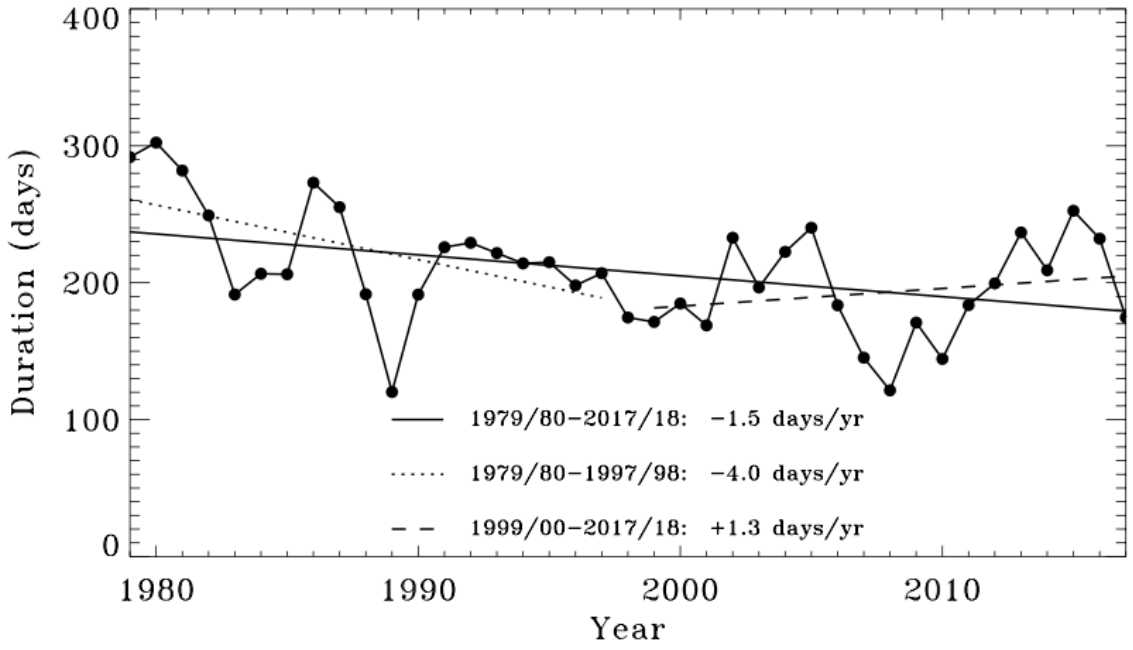


Figure 1. (a) Trend in winter air temperature (June, July, August; JJA) as recorded at Faraday/ Vernadsky Station (65.4 °S, 64.4 °W) from 1951 to 2017. The long-term linear trend (solid line: 1951-2017) is significant at the p <0.001 level, while the shorter-term trends (dotted: 1979-1997; dashed: 1999-2017) are not significant at the p <0.1 level. (b) Trend in the annual ice season duration determined using the GSFC Bootstrap version 2 sea ice concentration time series from Nimbus-7 SMMR and DMSP SSM/I-SSMIS and methods described in Stammerjohn and Maksym (2017). The trend was determined for the WAP continental shelf, extending from Anvers Island to Charcot Island. The long-term trend (solid line: 1979-2017) is significant at the p <0.05 level, while the shorter-term trends (dotted: 1979-1997; dashed: 1999-2017) are not significant at the p <0.1 level.

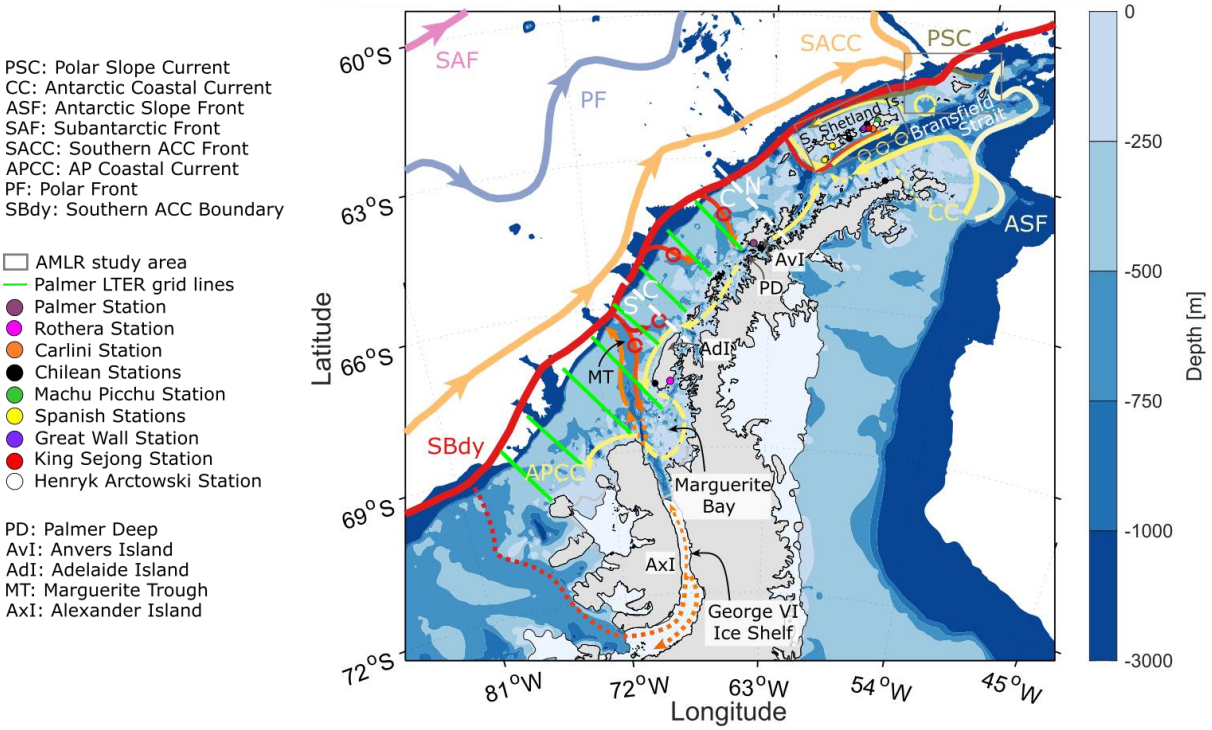


Figure 2. Map of the WAP showing the major sustained research efforts represented, delineation of the northern, central and southern sub-regions referred to in the text (white dashed lines; N = northern sub-region, C = central sub-region, S = southern sub-region), and the major circulation and bathymetric features of the shelf system. Modified from Moffat and Meredith (2018).

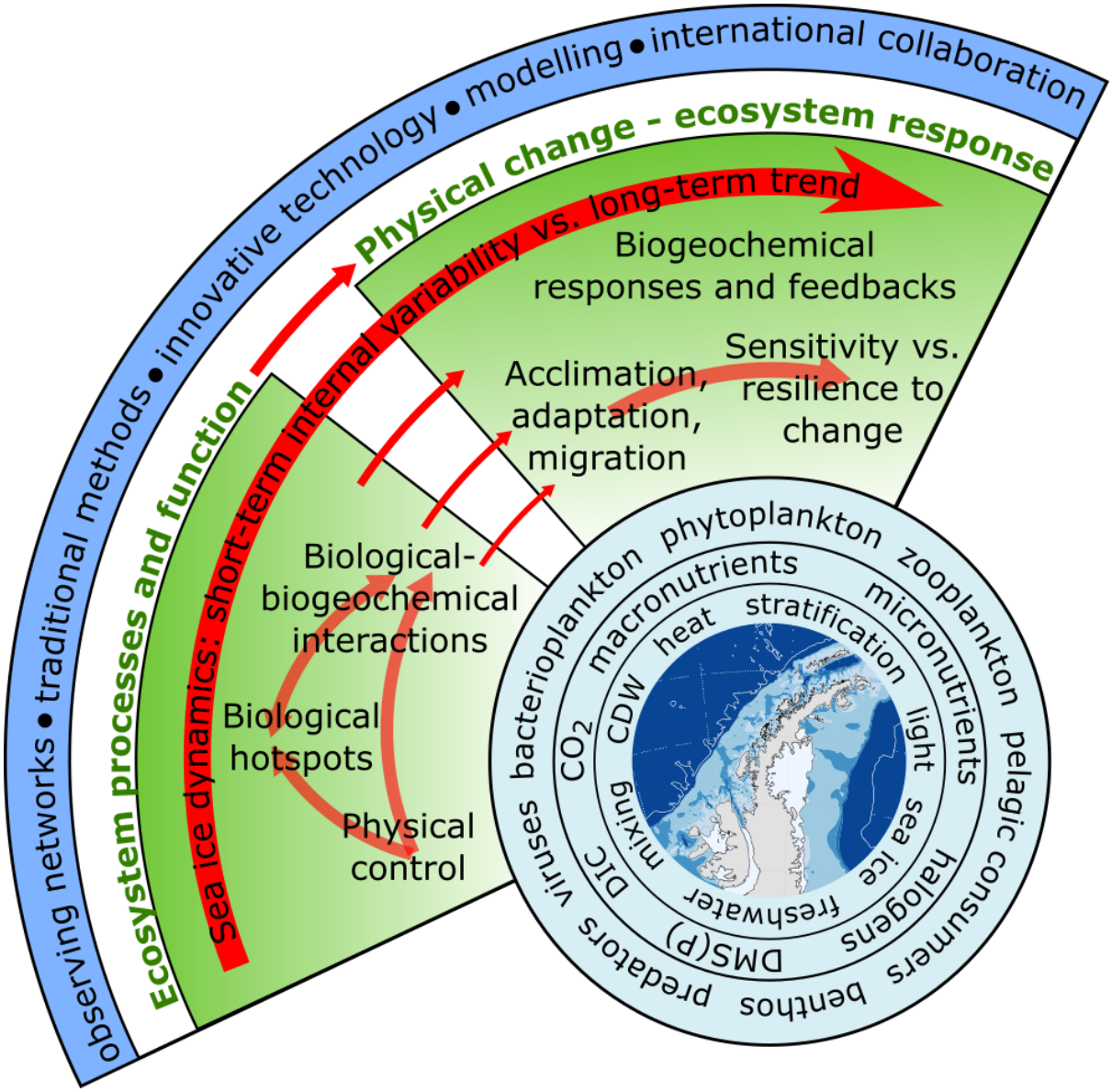


Figure 3: Infographic summarising the key components of the WAP marine system, the most important mechanisms and interactions in the context of the two overarching questions addressed in this paper, and the major priorities and approaches for future marine research at the WAP.

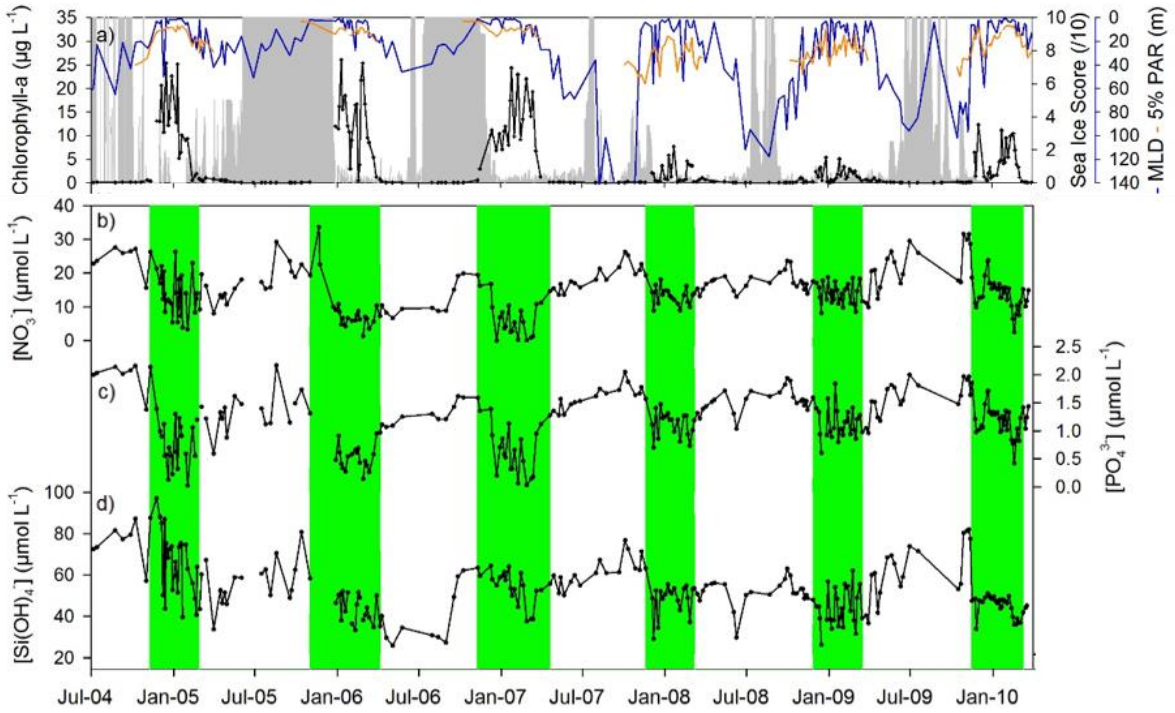


Figure 4. Time-series data from RaTS, July 2004 to April 2010, showing that high sea ice winters lead to shallow mixed layers, high chlorophyll and strong nutrient drawdown, whilst low sea ice years lead to deeper mixing, lower chlorophyll and less nutrient drawdown. (a) sea ice score (grey shading; coverage normalised to ice type, out of ten where ten is full fast-ice cover), mixed layer depth (MLD; blue line; depth where $\sigma = \sigma_{surface} + 0.05$ kg m^{-3}), 5 % PAR depth (orange line; depth where photosynthetically active radiation is 5 % of its surface value), chlorophyll *a* concentration at 15 m (black line). Nutrient concentrations (b) nitrate, (c) phosphate, (d) silicic acid. Green shading depicts the period when chlorophyll *a* >1 ug L^{-1}. Modified from Henley et al. (2017); sea ice, MLD, PAR and chlorophyll data from Venables et al. (2013).

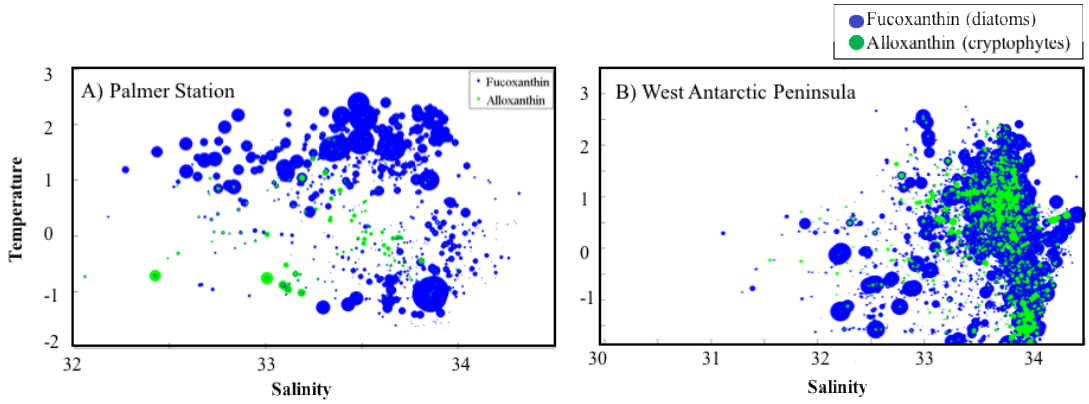


Figure 5. The relative presence of diatoms (from fucoxanthin, blue) and cryptophytes (from alloxanthin, green) plotted in temperature-salinity phase space for (a) Palmer stations B and E, and (b) the Palmer LTER grid. The size of the circles indicates the relative concentration of chlorophyll *a* for discrete samples. Modified from Schofield et al. (2017).

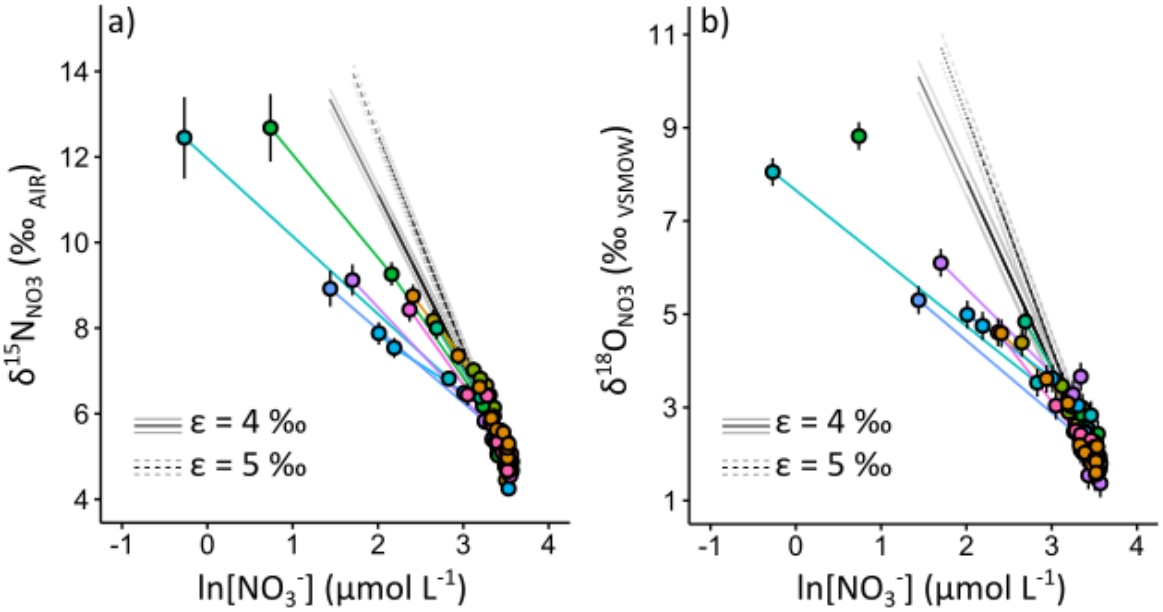


Figure 6. Relationships between nitrate concentration and its (a) nitrogen and (b) oxygen isotope composition, compared to modelled relationships based on nitrate uptake alone with fractionation factors (ε) of 4 and 5 ‰ (solid and dashed black lines, respectively). Both $\delta^{15}N$ and $\delta^{18}O$ plotting below the modelled lines indicates remineralisation of organic nitrogen where nitrate uptake is high, and subsequent nitrification in the subsurface water column. Data point colours represent different stations. Modified from Henley et al. (2018).

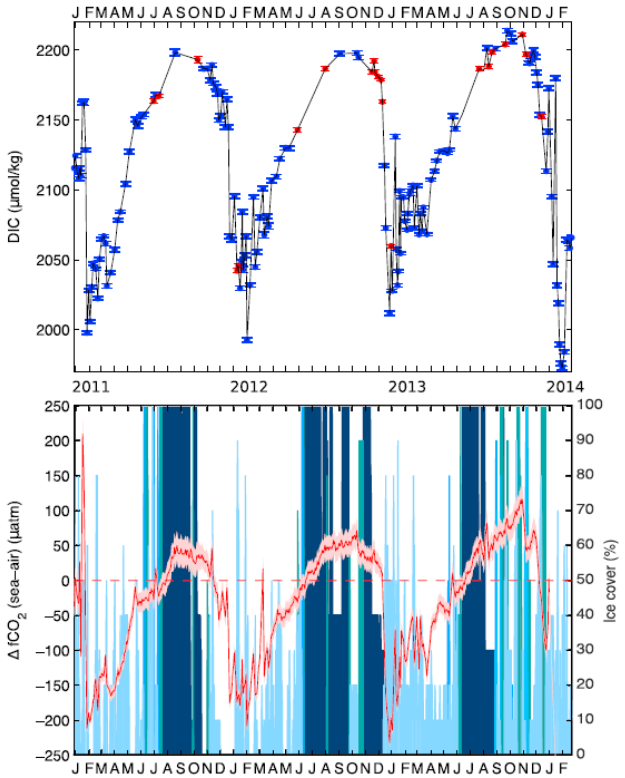


Figure 7. (a) Seasonal cycle of DIC from December 2010 to February 2014 at 15 m depth at RaTS sites 1 (blue) and 2 (red), both in Ryder Bay. Error bars are uncertainty (2SD) based on measurement precision. (b) Red solid line shows the seasonal cycle of the difference in fCO_2 between the sea and air (ΔfCO_2), with the pink shaded region representing approximate 95 % confidence from uncertainty analysis. Red dashed line shows $\Delta fCO_2 = 0$, where ocean CO_2 concentration is in equilibrium with the atmosphere. $\Delta fCO_2 > 0$ during winter indicates supersaturated conditions and an efflux of CO_2 to the atmosphere; $\Delta fCO_2 < 0$ during summer indicates undersaturated conditions and oceanic uptake of atmospheric CO_2. Blue bars show percentage ice cover, with dark blue representing fast ice, turquoise representing pack ice and light blue representing brash ice. Reproduced with permission from Legge et al. (2015).

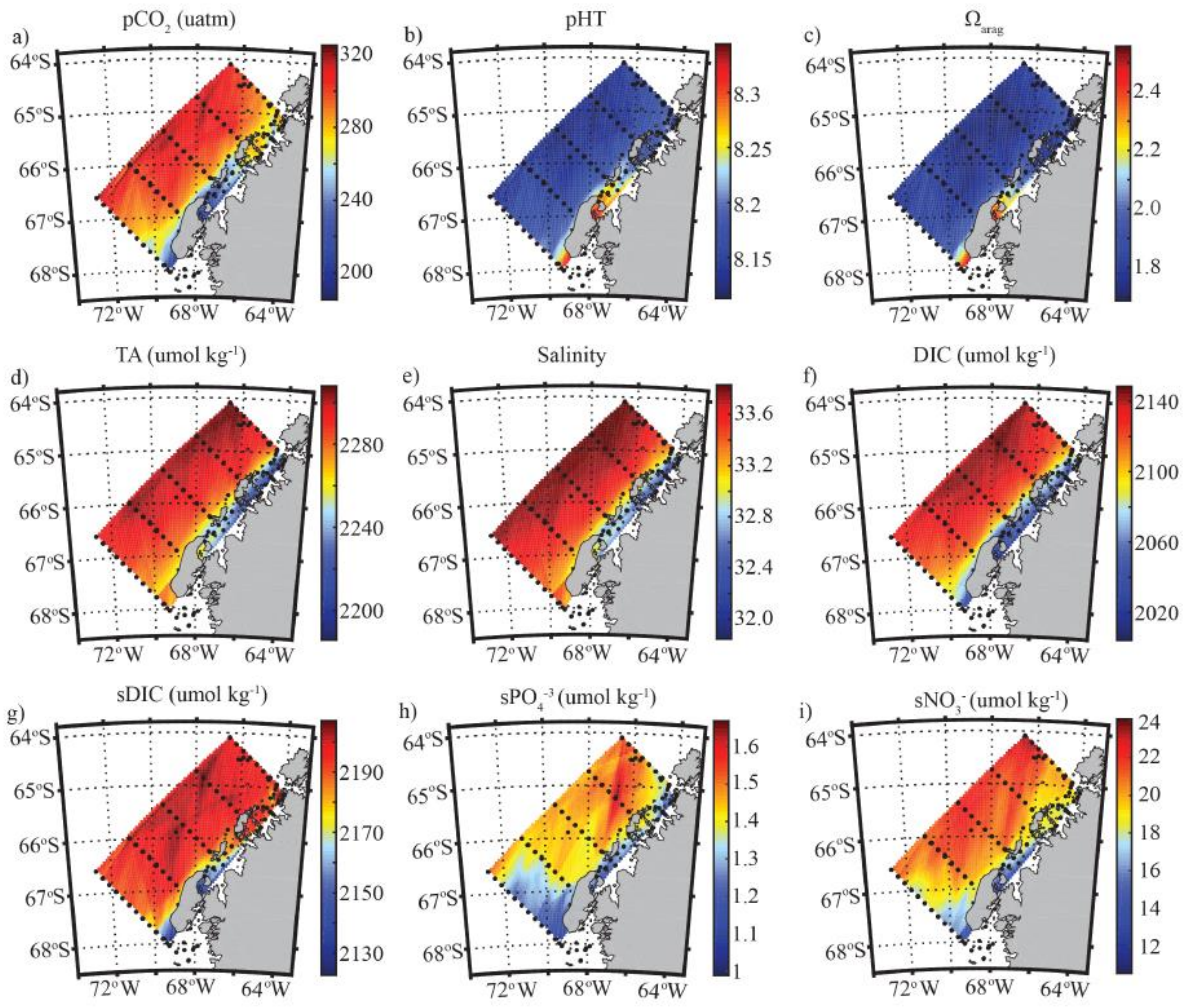


Figure 8. Summertime distribution of inorganic carbon system and other biogeochemical parameters in surface water for the Palmer LTER grid for the period 1993 to 2012, showing onshore-offshore and north-south gradients in carbonate chemistry, salinity and inorganic nutrients. Reproduced with permission from Hauri et al. (2015).

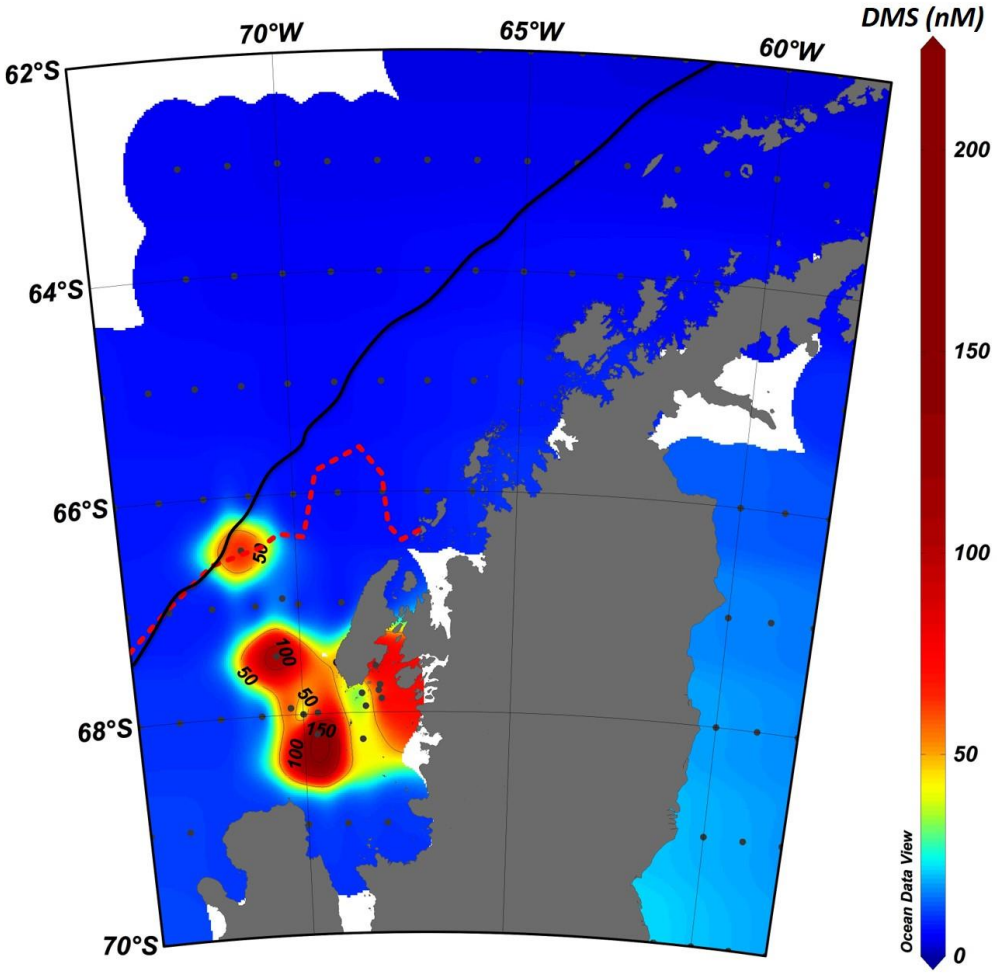


Figure 9. Surface DMS concentrations during cruise JR307 in January 2015 plotted on top of the 1x1 gridded January DMS climatology (Lana et al. 2011). JR307 data were calculated from filtered DMS(P) values (Stefels et al. 2018). The black line depicts the shelf edge; the red dotted line indicates the approximate position of the northern edge of the marginal ice zone during the second half of December 2014, immediately preceding the cruise.

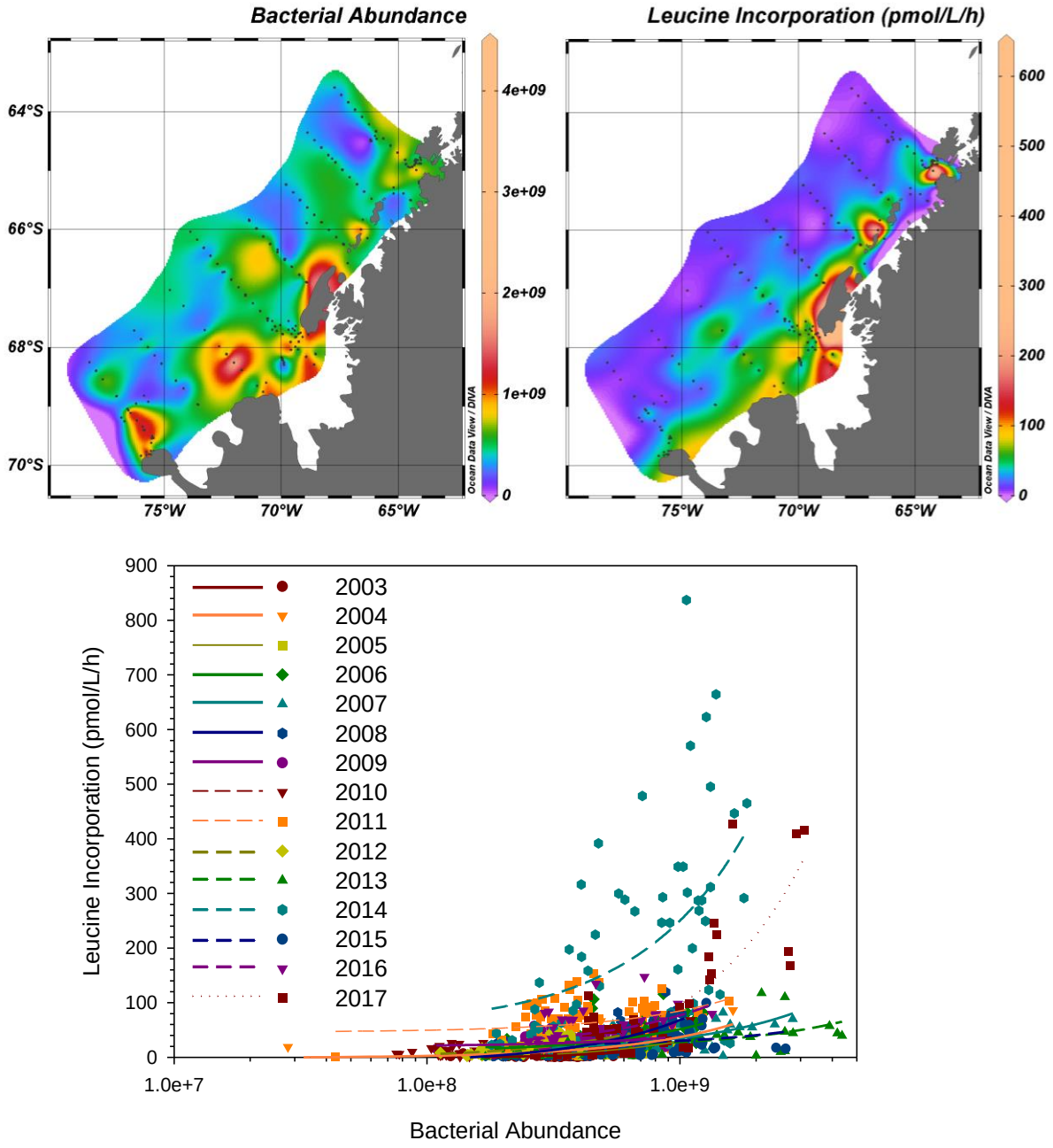
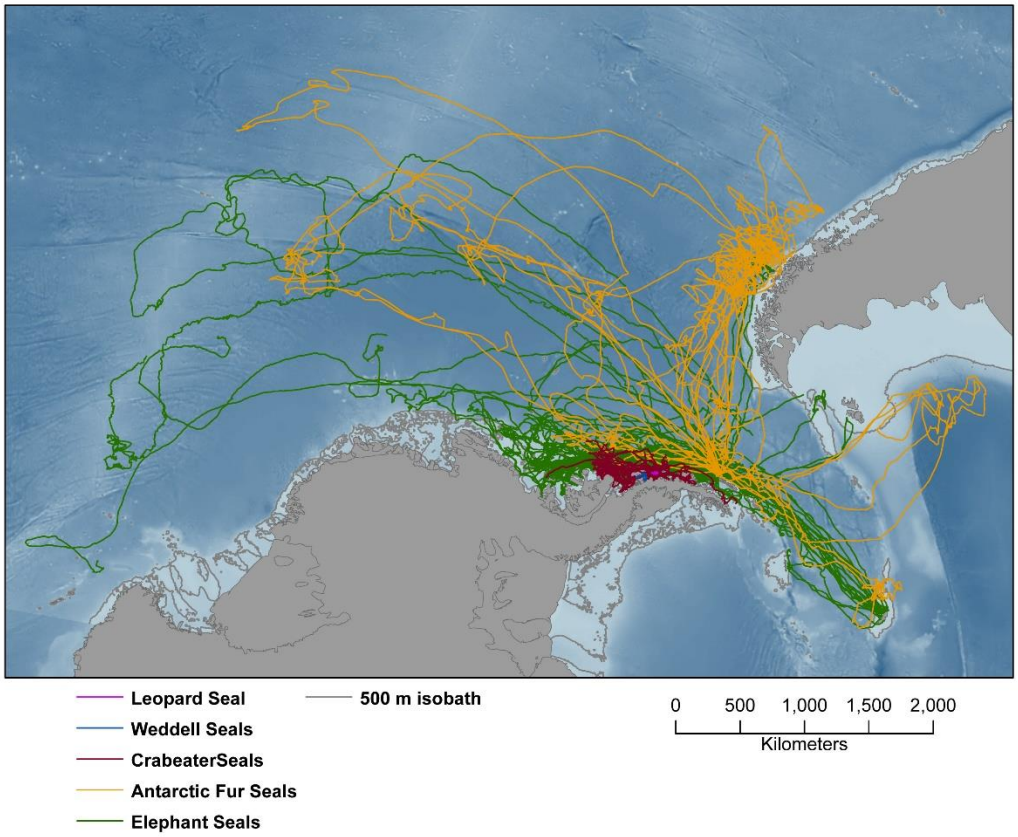


Figure 10. Long-term averages (2003-2017) for January of both bacterial abundance (top left) and production (top right) in the surface ocean (maximum depth 10 m), showing intense spatial heterogeneity with higher abundance and production in inshore regions, and higher abundance further south. Lower panel shows strong variability in bacterial production with abundance for individual January cruises, as per legend. All linear regressions are statistically significant (p <0.05), except for 2012. These data were collected as part of the Palmer LTER project and are updated from Ducklow et al. (2012a).



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1414 Figure 11. Tracks of crabeater seals (dark red) (Burns et al. 2004), elephant seals (green) (Huckstadt
1415 et al. 2012b), Weddell seals (blue), leopard seals (purple) (Costa et al. 2010), and fur seals (yellow)
1416 (Arthur et al. 2017) over an annual cycle from animal tracking tags.

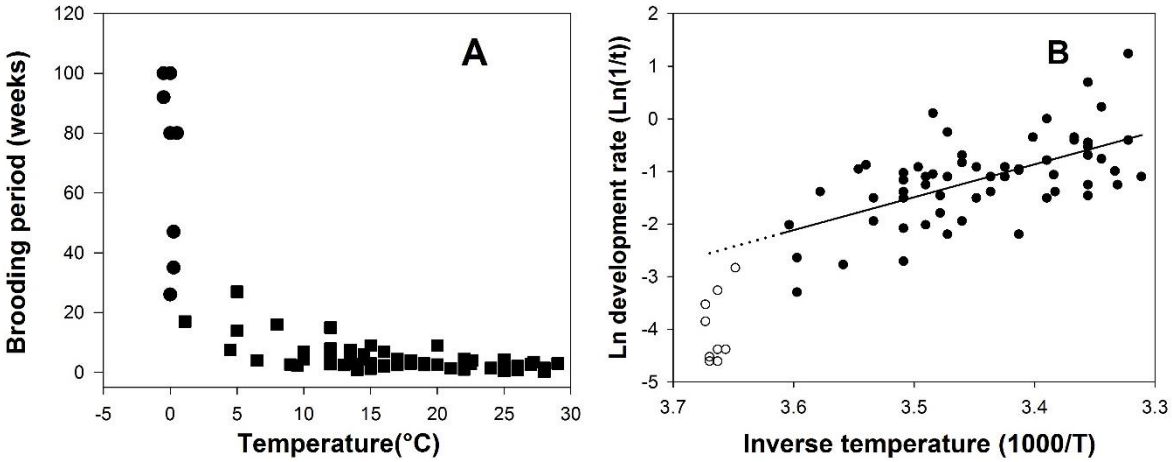

Figure 12. Brooding period and development rates of brooding marine gastropod snails at ambient temperatures for tropical to polar species. (a) Time from brood initiation to release (1/development rate) versus ambient temperature. In most cases, release is of crawling juveniles, but for two Antarctic species, release is of veliger larvae and development time to juvenile is approximately double that of brooding per se (Peck et al. 2006b). Data for 68 gastropod species, nine of which live at temperatures around 0°C, show the full development period to juvenile. (b) Arrhenius plot of Ln developmental rate to juvenile stage for brooding gastropod molluscs. Fitted line is for temperate and tropical species (filled circles; brooding rate (1/weeks) = 20.37 - 6.25 1000/T; $r^2 = 0.36$, F = 32.4, 58 df, p <0.001); Antarctic species fall significantly below. Reproduced from Peck (2018).

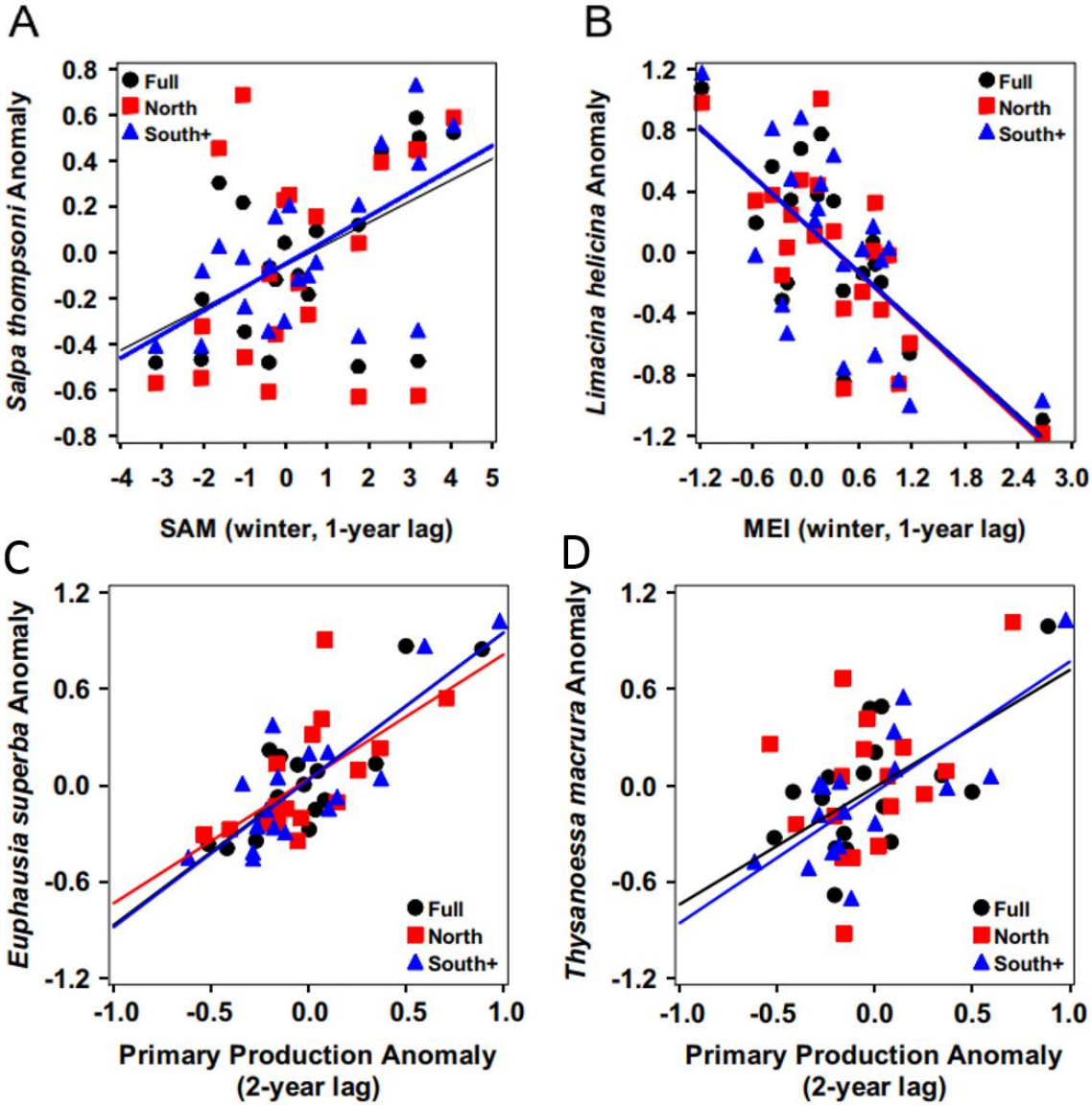

Figure 13. Relationships between annual abundance anomalies of specific zooplankton taxa on the Palmer LTER grid, 1993-2013, and sub-decadal climate oscillations and annual abundance anomalies of primary production. (a) *Salpa thompsoni* and SAM winter index from the year prior, (b) pteropod *Limacina helicina* and multivariate ENSO index (MEI) from winter the year prior, (c) krill *Euphausia superba* and primary production from two years prior, (d) krill *Thysanoessa macrura* and primary production from two years prior. Full refers to the full LTER grid, North refers to the northernmost three sampling lines, which are referred to as the central WAP sub-region in this paper, and South+ refers to the southernmost five sampling lines, referred to as the southern WAP sub-region in this paper (Figure 2). Modified with permission from Steinberg et al. (2015).

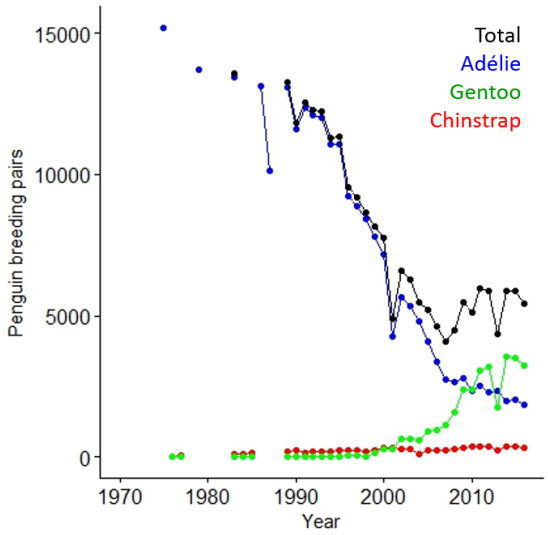

Figure 14. Population census data for Adélie, chinstrap and gentoo penguins in the Palmer Station region, 1975-2016. Updated from Ducklow et al. (2013).

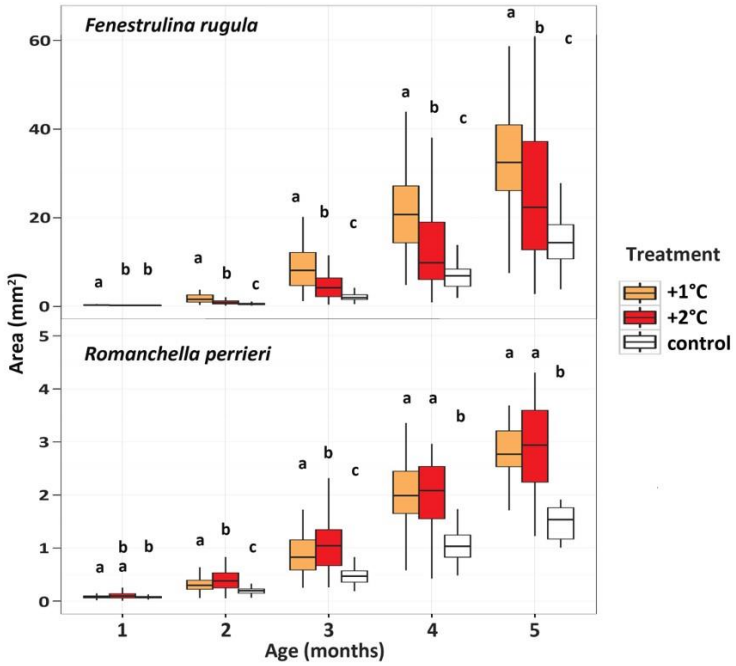

Figure 15. Effects of *in situ* warming on the growth of common epifaunal marine invertebrates on Rothera Point, Adelaide Island. Panels show area covered by the spatially dominant bryozoan (*Fenestrulina rugula*) and spirorbid (*Romanchella perrieri*) under warming (+1°C and +2°C) and control treatments, showing different growth rate responses between species. Data show the mean and interquartile range of panel surface area covered by a single colony (top) or individual (bottom). Different letters indicate significantly different areas per age ($F_{(1,9)}$ with p <0.01). Modified from Ashton et al. (2017).

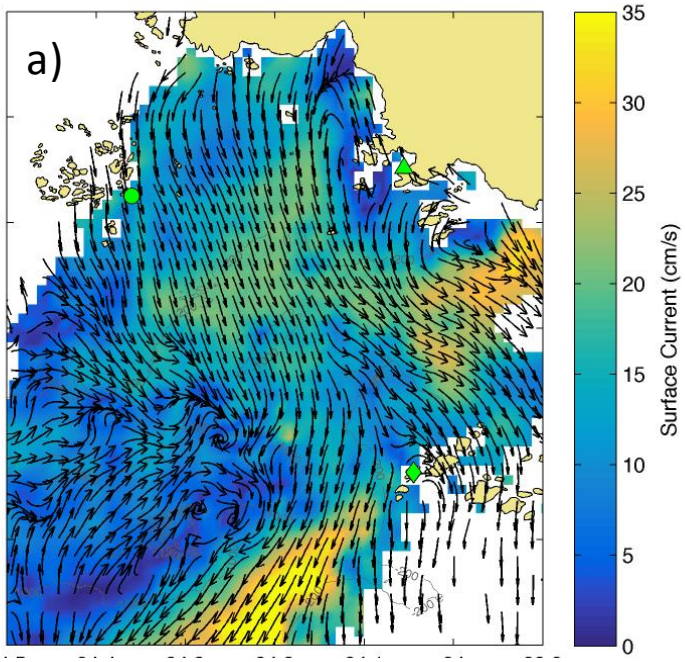

Figure 16. Hourly surface current map for the Palmer Station region for January 27, 08:00 GMT, 2015. The HF radar sites located at Palmer Station (green triangle) and the Wauwermans (green diamond) and Joubin (green circle) island groups are also shown.

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Table 1. Discipline-specific research objectives for the international community working along the WAP for the next 2-10 years

Ice dynamics and physical oceanography	Phytoplankton communities	Nutrient biogeochemistry	Climate-active gases	Microbial processes	Zooplankton dynamics	Higher trophic levels	Benthic ecosystems
Construct an accurate WAP shelf heat and salt budget over the complete annual cycle: *Eddy formation and onshelf CDW transport* *Cross-shelf water mass modification* *Mixing mechanisms and rates, especially during winter-spring/ summer ice retreat* Constrain oceanic processes modulating glacial retreat and impact of freshwater discharge on shelf properties and processes Determine relative influence of internal variability and climate change on property budgets, circulation and sea ice cover	Quantify the drivers of phytoplankton dynamics and diversity on seasonal timescales Identify potential species shifts driven by physical and chemical changes Conduct functional assessments of phytoplankton communities Elucidate the link between sea ice algal and pelagic communities and carbon fluxes Establish the influence of phenological changes on consumers and trophic structure	Construct accurate annual budgets of macro- and micronutrients for the WAP shelf: *Quantify nutrient fluxes onto, across and off the shelf* *Constrain the factors regulating autumn/winter nutrient resupply* *Quantify benthic-pelagic coupling through benthic nutrient recycling and exchange* *Assess sea ice and glacier chemistry, and meltwater influence on ocean chemistry* Identify the role(s) of micronutrients other than iron in primary production Discern the relative importance of new and regenerated production under changing conditions Describe seasonal patterns in organic nutrient dynamics in relation to phytoplankton and microbial processes	Quantify year-round air-sea exchange fluxes of CO_2, halogens and DMS along the WAP: *Assess the role of sea ice in modulating fluxes* Constrain the roles of sea ice, glacial melt and upwelling on gas concentrations and fluxes Estimate the timing of aragonite undersaturation and the sensitivity of carbonate chemistry, CO_2 fluxes and WAP ecosystems to ocean acidification Understand the response of halogen and DMS emissions to environmental change and expected shifts in community composition and phenology	Conduct functional assessments of microbial communities Define microbial provinces by species composition and function Estimate the resilience of the microbial food web to changing conditions Constrain the ecological role of viruses as mortality agents/loss factors and consequences for trophic transfer efficiency Elucidate the interactions between microbial communities and other ecosystem components Describe bacterial decomposition of macroalgal-derived organic matter	Assess mechanisms affecting zooplankton physiological tolerances, reproductive success and food web interactions Constrain micro-zooplankton assemblage composition and dynamics Understand zooplankton-mediated export via diel and seasonal vertical migrations Determine the importance of zooplankton-mediated export for benthic community production Quantify the role of benthic organisms as food sources for krill	Identify controls on juvenile recruitment and juvenile and adult survival Constrain the importance of foraging behaviour, prey availability and habitat requirements in influencing distributions, and their climate-driven biophysical controls Assess species' abilities to change distribution, diet and behaviour under altered conditions	Constrain rates of key processes e.g. adaptation and acclimation, geneflow within and between populations Evaluate benthic organisms' capacities to adapt to altered environments, especially sedimentation rates, pH and temperature Quantify the importance of benthic-pelagic coupling to phytoplankton productivity

Table 2. Discipline-specific approaches and innovations to address the key research objectives over the next 2-10 years

<table>
<tr><th>Ice dynamics and physical oceanography</th><th>Phytoplankton and microbial communities</th><th>Nutrient biogeochemistry</th><th>Climate-active gases</th><th>Zooplankton dynamics</th><th>Higher trophic levels</th><th>Benthic ecosystems</th></tr>
<tr><td rowspan="3">Moored time series of ocean currents and hydrographic properties along the shelf break

HF radar measurements of surface currents

Glider surveys shelf-wide, full-depth, year-round and targeting specific features

Improving sensor and geolocation accuracy of seal-borne CTDs

Observational and numerical modelling studies focused on ice-ocean interactions

Better representation of precipitation, run-off and glacial melt in ocean models

Further development of general circulation and coupled atmosphere-ice-ocean models</td><td rowspan="2">Incorporate genomics, proteomics and transcriptomics studies into existing monitoring programs to provide finer-resolution taxonomic data and understand unique functions

Advances in single-cell sequencing and cell-sorting capabilities

Expand culture collections of key species to reveal functional pathways and responses to change

Determine viral lysis rates in phytoplankton and microorganisms

Combine microbial and physical data to improve niche characterisation

Dedicated flux studies using sediment traps, radiogenic isotopes, stable isotope tracers, diatom biomarkers (e.g. $IPSO_{25}$)</td><td>Interpret physics data to estimate advective fluxes

Experiments to constrain uptake and cycling process rates

Conservative and non-conservative geochemical tracers (e.g. Ba, Al), stable and radiogenic isotopes, rare Earth elements

Glacier and meltwater chemistry measurements

Benthic flux estimates from porewater profiles and chamber experiments

Improved models of nutrient supply, uptake, recycling and loss</td><td>Development of pCO_2 mapping techniques specific to Antarctic coastal sites

Direct CO_2 flux measurements for sea ice and surface waters

Continuous DMS measurements by mass spectrometry

Rate measurements of gas production and conversion processes using isotope addition experiments</td><td rowspan="3">Species-level data collection at higher-resolution spatial scales, including vertical

Metagenomic, molecular and isotopic studies, especially to examine micro-zooplankton species composition and trophic role

Sampling over a greater range of size fractions, including micro-zooplankton

Dietary analysis of key species</td><td rowspan="3">Satellite and electronic tracking tags, motion-sensing tags, acoustic receivers

Additional sensors on tracking tags e.g. CTD, video

Stable isotope analysis of tissues, feathers, whiskers and stomach content

Remote-sensing tools e.g. drones, satellite imagery

Integration with physical data and models to constrain bio-physical controls on distributions and change over time</td><td rowspan="3">In-situ environmental manipulation experiments, repeated regularly

Long-term experiments over years and multiple generations

Stable isotope and biomarker analysis of benthic organisms to constrain food sources

Studies focused on benthic fluxes of dissolved and particulate constituents, connectivity and influence on water column biology and biogeochemistry</td></tr>
<tr><td colspan="2">Use of air-sea-ice chambers to develop process understanding</td></tr>
<tr><td colspan="3">Sea ice sampling campaigns with a focus on early spring, including algal, nutrient, carbonate chemistry, halocarbon and DMS(O/P) measurements</td></tr>
</table>

	Development and deployment of fluorometers and dissolved oxygen, nutrient, pCO_2 and other sensors on autonomous platforms e.g. gliders, AUVs, moorings	Expanded use of video plankton recorders and multi-frequency acoustics from ships and AUVs	